An investigation of some aspects of the transition from ectothermic to endothermic metabolism in vertebrates

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by Peter E. Wheeler

Being a thesis presented in candidature for the degree of Doctor of Philosophy in the University of Durham, 1984.

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ABSTRACT

The standard metabolic rates (SMRs) of 19 lizard and a single crocodilian species were measured at 30 °C, and 14 lizards at 37 °C. The basal metabolic rates (BMRs) of 8 mammalian species were also determined using similar techniques.

Although the inter-specific exponent relating BMR to body mass in rodents was close to the widely used value of 0.75, intra-specific exponents and that of the genus *Sorex* were lower. Intra-generic exponents of *Lacerta* and *Cordylus* are significantly higher than 0.75, and a general exponent of 0.85 is proposed for inter-specific comparisons of small lizards. Standard metabolic levels (SMLs) calculated using this exponent ranged from 0.096 to 0.230, at 30°C, demonstrating that lizards are not a metabolically homogeneous group. Mammalian BMLs varied from 2.108 to 11.096, and therefore the metabolic differences between this class and the reptiles cannot be described by a single factor.

The *in vitro* oxygen consumption rates were measured of liver, kidney, cardiac and skeletal muscle from lizards and mammals covering a range of body masses. Brain, lung and visceral smooth muscles were also compared in *Mus musculus* and *Cordylus jonesi*. All mammalian organs possessed higher metabolic rates than their reptilian equivalents. However, these differences, which varied considerably between tissues, were less than those of living animals. The reasons for the higher cellular and organismal metabolic rates of mammals are discussed.

Lacerta lilfordi and *Cordylus jonesi* acclimated to 20 °C displayed the same preferred body temperatures (PBTs) as lizards maintained at 30°C, despite experiencing partial compensation of their SMRs. Lizards allowed to behaviourally thermoregulate during their photophase possessed similar SMRs to those acclimated isothermally to the same background temperatures.

The PBTs of 4 European and 8 African lizard species were determined in a thermal gradient. Possible adaptative differences in saurian PBTs and SMLs are discussed in relation to their thermal environment.

CONTENTS

ACKNOWLEDGEMENTS

I am greatly indebted to Professor K. Bowler for help, advice and patience during his supervision of this project. The study was conducted whilst in receipt of a Science Research Council studentship, and I am grateful to Professor D. Barker for allowing me full use of the facilities of the Department of Zoology. In particular I would like to thank P. Hunter, P. Loftus, J. Summerill and T. Gibbons for help in maintaining the many diverse, and often difficult, animals throughout this work, and A. Bowman for assistance with electronics. I acknowledge the support of the Smith, Kline & French Foundation in the provision of equipment and the co-operation of the numerous individuals who made it possible for me to obtain the various animals used in the course of this study. Finally I would like to thank Mrs. Sue Abraham for her contribution to the preparation of this thesis.

CHAPTER 1

GENERAL INTRODUCTION

1.1 BRADYMETABOLIC AND TACHYMETABOLIC ORGANISMS

The majority of living organisms are bradymetabolic ('slow-metabolism'), producing insufficient heat from metabolic processes while at rest to regulate body temperature significantly above that of their surroundings. Such animals, which include all the invertebrates and lower vertebrates, are often described as being both poikilothermic and ectothermic. However, this is not always appropriate since it has been discovered that the temperature relations of many of these organisms are more complex than was once appreciated. Some species living in thermally heterogeneous surroundings are able to achieve some control of body temperature by shuttling between microclimates of differing environmental temperature (Heath, 1965, 1970). Such behavioural homeothermy is particularly well developed in many diurnal species of lizards, some of which are able to maintain body temperatures similar to those of mammals during the periods they are active (Stebbins & Barwick, 1968). A few bradymetabolic organisms are also able to utilise the large amounts of heat produced during muscular activity to raise core temperature above that of their environment, a condition known as exercise endothermy. This usually only occurs in very large animals which, as a consequence of their reduced surface area to volume ratio, possess thermal conductances low enough to retain sufficient heat to enable these temperature gradients to develop. Such exercise endotherms include some large fast-swimming fish (Carey, Teal, Kanwisher & Lawson, 1971), marine turtles (Friar, Ackman & Mrosovsky, 1972) and varanid lizards (McNab &

Auffenberg, 1976). Some invertebrates are also able to attain exercise endothermy, despite their much smaller body size, because of the heat produced by the intense metabolic activity of their flight musculature. In some insects, including the sphinx moth *Manduca*, this thermoregulatory mechanism has reached a high degree of sophistication, incorporating superficial insulation and control of the circulation of body fluids to regulate the rate of heat loss (Heinrich, 1971).

The thermal physiology of the higher vertebrates is fundamentally different. These animals are able to continually modulate their much higher levels of endogenous heat production to maintain a near constant body temperature, and are consequently both homeothermic and endothermic. These animals are described as tachymetabolic ('fast-metabolism'), the only two extant groups being the mammals and birds. This more advanced thermoregulatory physiology allows most modern eutherian mammals to maintain body temperatures of 35 to 40°C, while the more primitive marsupials and monotremes regulate at lower temperatures in the range 30 to 35°C. Birds generally maintain core temperatures higher than those of mammals; non-passerines approximately 37 to 44°C and passerines 39 to 44°C (Precht *et al.*, 1973).

1.2 THE EVOLUTION OF TACHYMETABOLISM IN THE PHYLOGENY OF THE VERTEBRATES

Tachymetabolism appears to have been developed at least twice in the course of vertebrate evolution. The older of the two extant tachymetabolic groups are the mammals which first appeared during the Triassic, more than 180 million years ago (Hopson, 1969; Hopson & Crompton, 1969). The ancestry of this class is particularly well documented in the fossil record and can be traced back through the

Triassic and Permian mammal-like reptiles to the primitive Cotylosauria of the Carboniferous (Romer & Price, 1940; Romer, 1966). The first group of mammal-like reptiles to evolve were the Pelycosauria, some of which, like the sail-backed *Dimetrodon*, attained lengths in excess of 3 m. Later these were replaced by the more advanced Therapsida, which radiated into many diverse herbivorous and carnivorous forms during the Middle and Upper Permian. The carnivores included the Cynodontia which are thought to have been ancestral to the mammals (Hopson & Crompton, 1969). During the evolutionary history of the therapsids leading to the mammals there was a marked reduction in body size, since all the known earliest forms were small shrew-like animals measuring only a few centimetres in length (McNab, 1978). During the later Mesozoic the mammals radiated into several orders, although only three of these survived the end of the Cretaceous and have living representatives. Of these the placental mammals (Eutheria) and marsupials (Metatheria) are thought to share a common ancestry, while the origins of the monotremes (Prototheria) are less certain. Although it has been suggested that the monotremes evolved independently from the therapsids (Simpson, 1959; Kermack, 1967; Augee, 1978) other workers favour a monophyletic origin for the mammals (Hopson, 1969; Hopson & Crompton, 1969).

A wide range of characteristics distinguish mammals from their reptilian ancestors. These include the possession of an erect posture, squamosal-dentary jaw joint, large relative brain size, lactation, superficial insulation and tachymetabolism. For convenience the dividing line between the mammals and reptiles is usually defined on the basis of jaw articulation (Romer, 1966), since this can be easily determined from fossil remains. It is extremely unlikely that all the

other mammalian features were acquired simultaneously, and attempting to establish when tachymetabolism evolved is more difficult. Bakker (1971, 1975) and de Ricqlès (1974, 1976) have proposed that the therapsids may have already attained at least some degree of tachymetabolism, a view not supported by other workers (McNab, 1978; Crompton, Taylor & Jagger, 1978).

The birds appear to have evolved tachymetabolism independently, since their reptilian ancestors are only distantly related to those of mammals (Kemp, 1980). The oldest known bird, *Archaeopteryx*, dates from the Upper Jurassic, at least 40 million years after the appearance of the first mammals (Romer, 1966). Birds evolved from the Archosauria, an advanced group of reptiles the radiation of which during the Triassic was probably responsible for the decline of the therapsids. It was the earliest group of archosaurs, the Thecodontia, which gave rise to the crocodilians, pterosaurs, ornithischian, saurischian dinosaurs, and ultimately the birds. The traditional view was that the birds descended directly from the early thecodont stock (Heilmann, 1926). However, it is now widely accepted they evolved from the Coelosauria, a group of small saurischian dinosaurs (Ostrom, 1973, 1974).

It had been generally assumed that all the extinct archosaurs were bradymetabolic, and that tachymetabolism was only attained with the evolution of the birds. The recent challenging of this view has provoked a major controversy over the thermal relations and taxonomy of these animals. Studies of bone histology, community structure, posture and palaeolatitudinal distribution have all been cited as evidence that both the ornithischian and saurischian dinosaurs possessed an advanced tachymetabolic physiology like mammals and birds

(Ostrom, 1969; Bakker, 1971, 1972, 1975; de Ricqlès, 1974, 1976), although this interpretation has been strongly contested (Bennett & Dalzell, 1973; Fedducia, 1973; Thulborn, 1973). Examined individually none of these arguments can yet be taken as conclusively demonstrating tachymetabolism in dinosaurs, yet when taken together they do indicate that the metabolic physiology of these animals was probably more advanced than had previously been thought. The evidence for tachymetabolism among pterosaurs is even more compelling since traces of an insulatory layer of body hair have been found in fossil remains of *Sordes pilosus* (Sharov, 1971). Also, it is extremely difficult to reconcile the high energy turnover demanded by powered flight in vertebrates with a primitive reptilian physiology. Therefore, even accepting a coelosaurian origin for the birds, if these new ideas are correct then either tachymetabolism must have evolved independently at least twice in the archosaurs or the common thecodont ancestors of the pterosaurs and dinosaurs were themselves tachymetabolic. If the later thecodonts were tachymetabolic then this must have been acquired after the crocodilians had split from the other archosaurs, or alternatively bradymetabolism has been secondarily evolved by this group, possibly as an adaptation to an aquatic mode of life.

Bakker & Galton (1974) considered the difference between brady-metabolic and tachymetabolic animals so fundamental that they proposed a reclassification of the vertebrates in the light of these new ideas about the thermoregulatory physiology of the extinct therapsids and archosaurs. They suggested that the Therapsida should be placed with the mammals in the class Theropsida. A new class, the Archosauria, was erected to accommodate the pterosaurs, dinosaurs and birds,

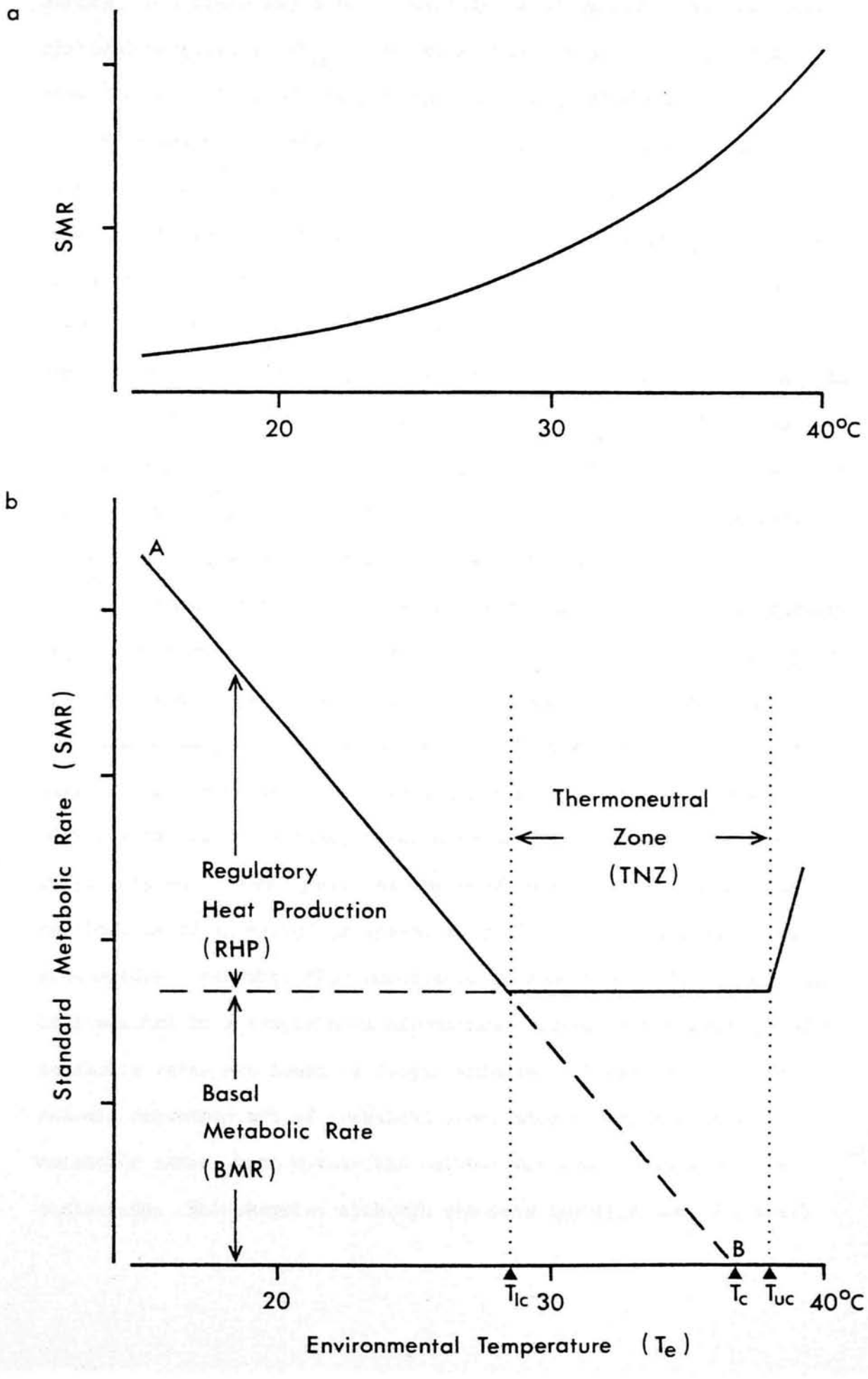
together with their advanced thecodont ancestors. However, this or similar proposed taxonomic changes (Desmond, 1975) are unlikely to be adopted until the evidence of tachymetabolism in these extinct groups has gained more widespread acceptance.

1.3 METABOLIC HEAT PRODUCTION IN TACHYMETABOLIC VERTEBRATES

The pattern of endogenous heat production by both mammals and birds differs from that of the reptilian ancestors in two fundamental ways. The first is qualitative, and concerns the influence of environmental temperature (T_e) upon the standard metabolic rate (SMR) of the animal. In reptiles, like all other bradymetabolic organisms, a decreased T_e simply causes a fall in SMR (Fig. 1.1a). This is because biochemical and physiological processes proceed more slowly at lower temperatures, due to the reduced heat energy content of the system. The factor by which SMR changes when temperature is raised by 10°C can be described by a temperature coefficient, or Q_{10} value. For most bradymetabolic animals Q_{10} values of overall SMR are usually between 1.5 and 3. Mammals and birds respond to a drop in T_e very differently, since they are able to increase their SMR to maintain a constant body temperature (Fig. 1.1b). As T_e falls below the regulated core temperature (T_c) of a tachymetabolic animal it can initially maintain homeothermy by reducing the rate at which heat is lost to the environment. This is primarily achieved by peripheral vasoconstriction and increasing the effective thickness of the superficial insulation. The range of environmental temperatures across which the animal can achieve homeothermy solely by controlling thermal conductance is described as its thermoneutral zone (TNZ). Within this TNZ the SMR of the animal is at its minimum level, termed basal metabolic rate

Figure 1.1 The influence of environmental temperature on the standard metabolic rates of (a) bradymetabolic and (b) tachymetabolic organisms (for explanation see text 1.3).

Fig. 1.1


a
SMR
20
30
40°C
b
A
Standard Metabolic Rate (SMR)
Thermoneutral
Zone
(TNZ)
Regulatory
Heat Production
(RHP)
Basal
Metabolic Rate
(BMR)
B
20
T_{lc}
30
T_c
T_{uc}
40°C
Environmental Temperature (T_e)

(BMR). However, the extent to which thermal conductance can be reduced is limited and when it has reached its minimum, at the lower critical temperature (T_{lc}), the animal must respond to any further lowering of T_e by increasing endogenous heat production.

This ability to generate additional regulatory heat production (RHP) to replace heat lost to the environment is found only in tachymetabolic animals. The rate at which RHP increases as T_e is reduced, the gradient of the line A-B in Fig. 1.1b, describes the thermal conductance (C) of the animal. The line should extrapolate on the abscissa to a value of T_e equivalent to its core temperature. This is because if T_c and T_e were the same there would be no net heat loss, and consequently none would need to be produced to maintain homeothermy. Of course this situation can never occur in practice since the animal is unable to reduce its heat production below BMR.

The second distinction between bradymetabolic and tachymetabolic animals relates to quantitative differences in the metabolic rates of the two groups. As the terms imply, the BMRs of birds and mammals are considerably higher than the SMRs of bradymetabolic animals at similar body temperatures. However, making quantitative comparisons of metabolic rates is complicated because this parameter is allometrically related to body mass. As expected, within a taxonomic group as the size of an animal increases so does its total resting oxygen consumption. However, this additional consumption is less than would be predicted by a simple mass dependency. Consequently mass specific metabolic rates are lower in larger animals. Therefore, unless the animals concerned are of identical size, direct comparisons of metabolic rates, both within and between taxonomic groups, can be misleading. For example, although the mass specific SMR of a small

lizard at 37°C will be considerably lower than the BMR of a similarly sized rodent, it will actually be higher than that of a much larger mammal such as an ungulate.

This relationship between metabolic rates and body mass can be described in birds and mammals by an allometric equation of the form;

$$BMR(ml\ O_2/h) = a.\ Mass\ (g)^b$$

and in lower vertebrates and invertebrates, at a specified body temperature;

$$SMR\ (ml\ O_2/h) = a.\ Mass\ (g)^b$$

Often the relationship is expressed in terms of mass specific metabolic rate, in which case for tachymetabolic vertebrates;

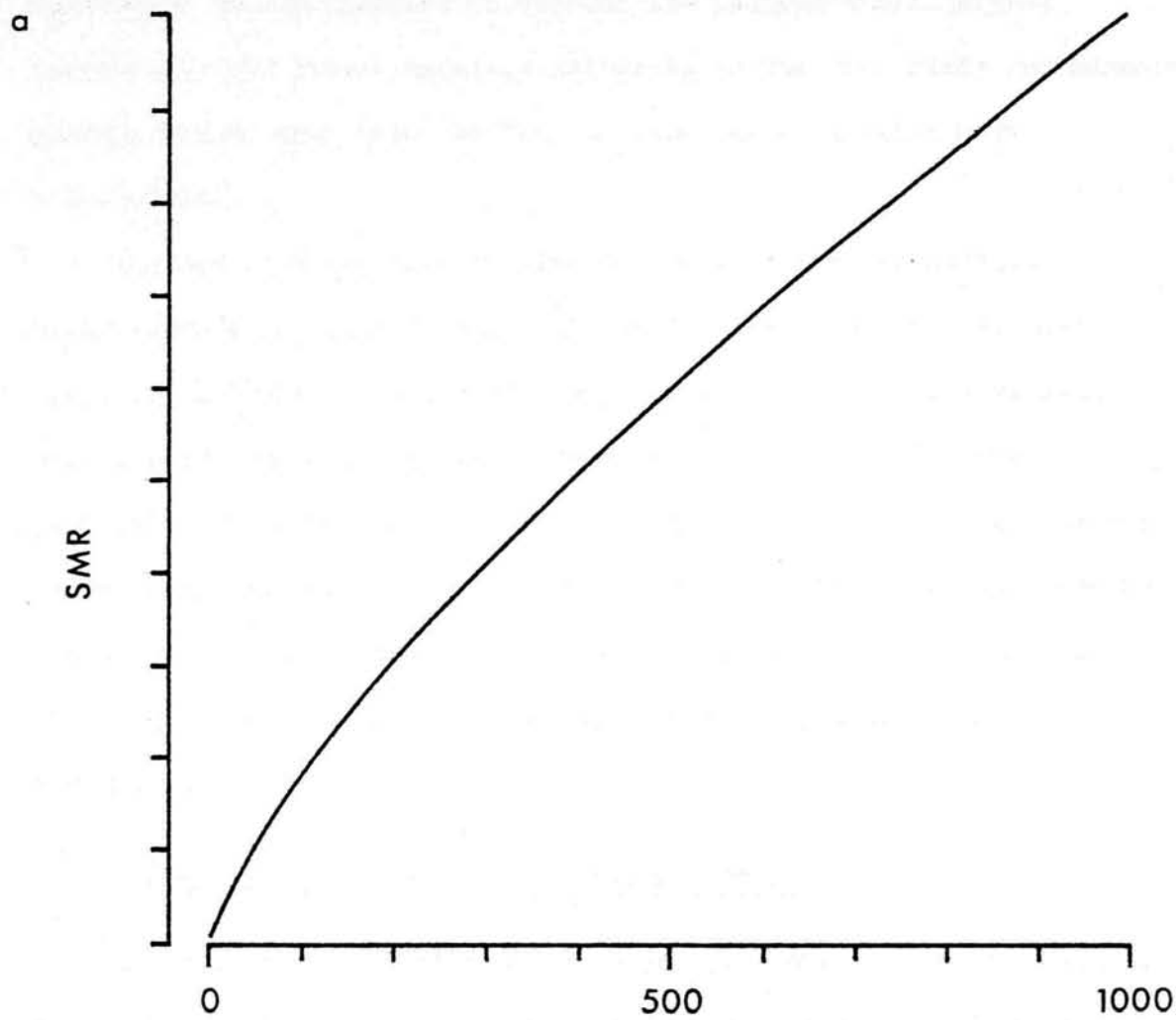
$$BMR\ (ml\ O_2/g.h) = a.\ Mass\ (g)^{b-1}$$

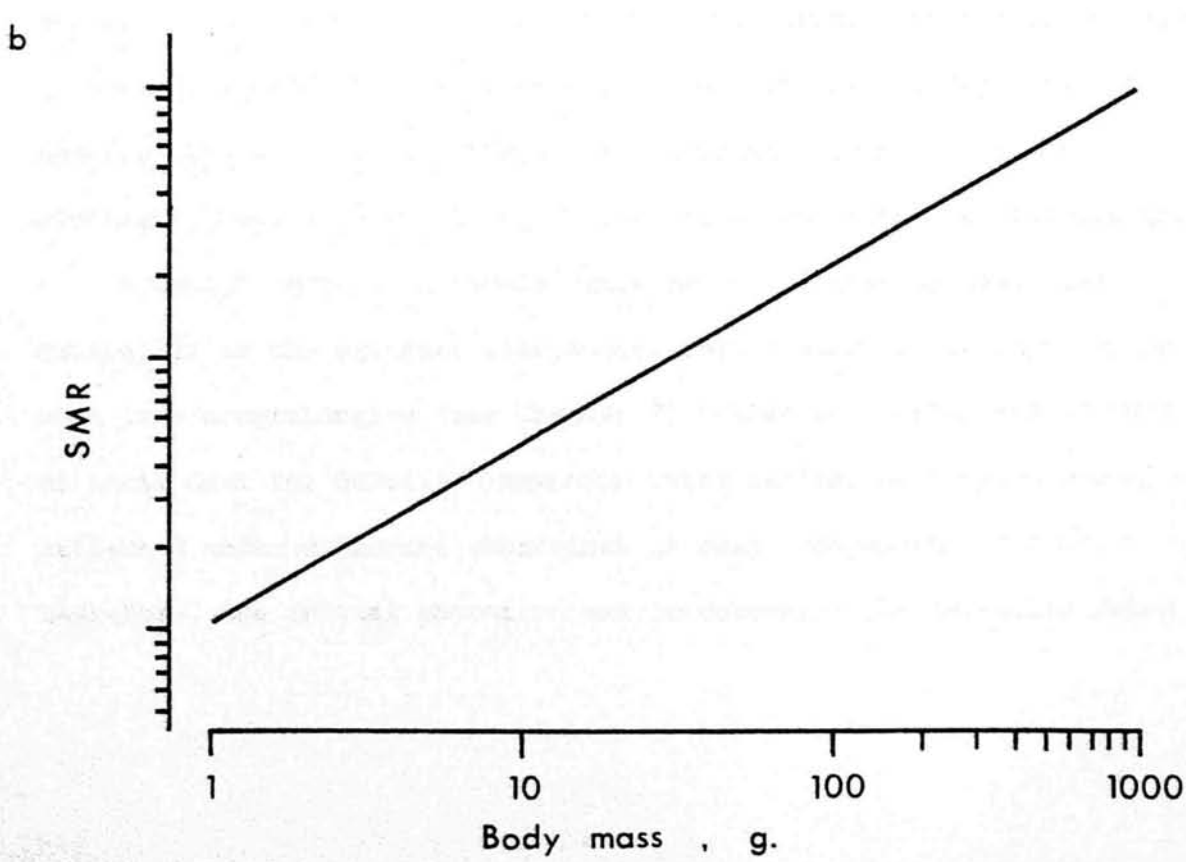
The values of a and b are constants for a particular group of animals. These are usually calculated by linear regression of logarithmically transformed data (Fig. 1.2b). As discussed above, the exponent b is usually less than unity. For example, the general exponent used for inter-specific comparisons of mammalian BMRs is usually taken as 0.75 (see Chapter 3.3.2). Within a taxonomic group the value a is an index of resting heat production independent of the animal's body mass. Among tachymetabolic vertebrates this parameter is termed basal metabolic level (BML). The corresponding parameter for bradymetabolic animals is standard metabolic level (SML), and in this case body temperature must of course be specified. If groups possess similar exponents then differences in their resting metabolism can be quantified by comparing their metabolic levels. Therefore, the second

Figure 1.2 (a) Within a taxonomic group the total standard metabolic rate of an animal is allometrically related to its body mass and can be described by an equation of the form $SMR = a.Mass^{b}$, where the exponent, b, is usually less than unity.

(b) Plotting the data on logarithmic axes produces the linear relationship log SMR = b.log Mass + log a. In the present study the values of the constants a and b were calculated by linear regression analysis of logarithmically transformed data.

Fig. 1.2





difference in heat production between the tachymetabolic higher vertebrates and their reptilian ancestors is that the birds and mammals possess higher BMLs than the SMLs of reptiles at similar body temperatures.

The use of these high regulated levels of heat production for thermoregulation would be extremely energetically expensive, particularly for smaller species with high surface area to volume ratios, unless these animals possessed lower thermal conductances than reptiles. Consequently the vast majority of birds and mammals have a covering of feathers or fur, which reduces heat loss from the body by trapping a boundary layer of air next to the skin. The effective thickness of this insulation can be altered by raising and lowering the pelage.

1.4 AIMS AND OBJECTIVES OF THE PRESENT STUDY

The aim of this study was to investigate one of the key steps in the evolution of tachymetabolism by mammals. As already discussed, the pattern of endogenous heat production in bradymetabolic and tachymetabolic animals differs in two ways. This study concentrates on the quantitative difference in metabolic level between the reptiles and mammals, rather than the ability of the latter group to produce additional heat in response to a lowering of environmental temperature.

Although there is a considerable amount of data on mammalian metabolism in the existing literature, that available for reptiles is much less comprehensive (see Chapter 2). Also the usefulness of much of these data for detailed comparative work is limited since they were collected under differing conditions in many independent studies. Therefore, the initial objective was to determine the metabolic rates

of reptiles and mammals, across a range of body masses, using standard procedures and techniques (Chapters 2 & 3). This enabled the exponents relating metabolic rate to body mass within the two groups to be calculated and the differences between the BMLs of mammals and the lower SMLs of reptiles, at a similar body temperature, to be accurately quantified. The second objective of the present study was to start working towards an understanding of the physiological and biochemical basis of these differences. This required establishing the extent to which the higher metabolic levels of mammals are due to fundamental differences in cellular metabolism. To answer this question the metabolic rates of a range of isolated reptilian and mammalian tissues were compared (Chapter 4).

Before undertaking a study of this kind, particularly when the intention is to make evolutionary inferences, some consideration must be given as to which groups of animals are to be used. Ideally comparisons would be made between primitive mammals and representatives of the reptilian group ancestral to them. This is obviously not possible since these forms are long extinct, and therefore the work must be based on comparative studies of living species.

The crocodilians and the birds are probably the two most closely related groups of bradymetabolic and tachymetabolic vertebrates. However, using these animals would present two major problems. The first is a purely practical one since it would not be possible to obtain crocodilians in sufficient quantities for a study of this type. Second, and more importantly, although birds and mammals both possess high regulated levels of endogenous heat production there is no reason to assume that the physiological and biochemical mechanisms by which this is achieved are the same in the two groups.

There are no obvious reptiles with which to compare the physiology of mammals, since they are not closely related to any of the living groups. It cannot be assumed that the metabolism of all living species is necessarily representative of the primitive reptiles ancestral to the mammals, as they too have continued to evolve for the last 250 to 300 million years. Therefore, to ensure that mammals are not being compared with a specialised atypical group of reptiles data were obtained from a wide range of species before attempting to make any generalisations about reptilian metabolism. However, it was decided to confine the study to lizards and crocodilians, since both chelonians and snakes are morphologically very different from mammals; a large proportion of the total body mass of chelonians consists of a relatively metabolically inert bony shell, and in addition to lacking limbs with the associated musculature, the anatomy of the internal organs of snakes is rather specialised due to their extremely elongate shape. Rhychocephalians possess a lizard-like morphology and their retention of many primitive characters would make their inclusion in a comparative study extremely desirable. However, the only surviving representative, the tuatara *Sphenodon punctatus*, is an endangered species, and therefore neither suitable nor obtainable for a study of this kind.

Therefore during the early stages of this study a substantial body of data was collected on the metabolic levels of a large number of lizard species. This demonstrated that they were a more metabolically diverse group than had previously been appreciated. It was therefore decided to take advantage of the wide range of species which had been assembled to explore questions relating specifically to reptilian thermobiology, in addition to the comparative work with

mammals. Consequently, experiments were conducted to investigate the acclimatory (Chapter 5) and adaptative (Chapter 6) relationships between both the SMLs and preferred body temperatures (PBTs) of lizards and their thermal environment.

CHAPTER 2

THE STANDARD METABOLIC LEVELS (SMLs) OF LIZARDS AND CROCODILIANS

2.1 INTRODUCTION

Since the first reported measurements of the metabolic rate of a lizard by Regnault & Reiset (1849) many studies have been conducted on a large number of reptilian species. With the accumulation of these data several attempts have been made to determine general relationships between metabolic rate and body mass in lizards (Dawson & Bartholomew, 1956; Bartholomew & Tucker, 1964; Templeton, 1970; Bennett & Dawson, 1976). Among the aims of this work were to establish whether the saurian exponent differs from the generally accepted value 0.75 relating basal metabolic rate to body mass in birds and mammals (Kleiber, 1961; Lasiewski & Dawson, 1967), and to quantify the differences in metabolic levels between the reptiles and these two groups of higher vertebrates.

The most comprehensive set of equations were produced by Bennett & Dawson (1976). These were calculated by regressing measurements made at 20, 30 and 37°C from many of the studies conducted during the previous eighty years. The resulting equations describing the metabolic rates of lizards were at 30°C;

$$MR\ (ml\ O_2/h) = 0.240.Mass\ (g)^{0.83}$$

and at 37°C;

$$MR\ (ml\ O_2/h) = 0.424.Mass\ (g)^{0.82}$$

However, there are problems associated with combining data from independent studies. Unwanted variation is introduced from

differences in experimental techniques and inadequate standardisation of conditions known to influence reptilian metabolic rates. Factors which have been identified as affecting determinations of resting metabolism include; environmental temperature, nutritional condition (Roberts, 1968; Coulson & Hernandez, 1980), time of day (Roberts, 1968; Songdahl & Hutchinson, 1972; Jameson *et al*, 1976) lighting conditions during the experiments (Craggs, 1978) and the state of thermal acclimation (Vance, 1953; Dawson & Bartholomew, 1956; Maher & Levedahl, 1959). To obtain some degree of comparability Bennett & Dawson (1976) selected data only from studies in which determinations were made from lizards resting in the dark during their diurnal phase. However, these criteria do not adequately standardise all the important variables. For example, dietary and acclimation state, when reported, varied considerably between the studies from which data were taken (The effects of thermal acclimation on saurian metabolic rates are discussed in Chapter 5.4.2).

A second potential source of error in the analysis of Bennett & Dawson (1976) is that they treated the lizards as a metabolically homogeneous group and produced their equations by regressing together data from all species. This assumes that the observed variations in metabolic rates of lizards of similar body mass were due simply to differences in experimental procedure. However, if some of this variation represents real differences in metabolic level between groups of lizards such a treatment of the data would be inappropriate; the metabolic rates of the lizards could not be adequately described by a single regression equation and there would be an inaccuracy in the estimate of the exponent if lizards of differing metabolic level were not equally represented in the samples across the entire

body mass range.

In view of these problems with the existing equations it was considered necessary to undertake a comprehensive re-examination of the relationship between resting metabolic rate and body mass in lizards. To ensure that all the data produced are comparable, strict standardisation of conditions and methodology was maintained for the determinations of all species.

The criteria of using resting animals maintained in the dark during their diurnal phase were further extended to standardise dietary state and thermal acclimation. In this study all animals were in a post-absorptive condition and acclimated, over a period of many weeks, to a temperature of 30°C. This temperature was selected because it can be tolerated by a wide range of species for long periods, and also much of the existing data on reptiles relate to measurements at 30°C. For comparisons with mammals there is a case for using an acclimation temperature of 37°C, since tissue temperatures in the two groups would then have been similar in the period before determinations were made. However, a lower temperature regime was chosen as not all the reptilian species used could tolerate prolonged exposure to such a high environmental temperature.

Previous studies have used a variety of techniques to measure reptilian metabolic rates. Since it is technically much easier to measure gaseous exchange than heat production most studies have utilised indirect, rather than direct, calorimetry. For this study it was decided to use indirect calorimetry by measuring the oxygen consumption of the animals. An open circuit system was used in preference to a closed or manometric one, since this allows the experimental animal to be maintained for long periods in a relatively

constant gaseous environment. Oxygen uptake was monitored by paramagnetic analysis of the effluent gas from the system. This technique has the advantage of permitting semi-automatic recording of the metabolism of a single animal continually over long periods of time without the need for frequent re-calibration. Another consideration was that this system is also suitable for use with small mammals, thereby allowing direct comparison of data produced by identical techniques between the two groups. Determinations of standard metabolic rate (SMR) were made from all species of reptiles at their acclimation temperature of 30°C. Most species, which could tolerate the higher temperature, were also measured at 37°C to enable direct comparisons to be made with the basal metabolic rates of mammals.

As many species of which sufficient numbers of individuals could be obtained were used. Particular attention was given to forms which had not previously been studied, as the existing literature shows a distinct bias towards families well represented in North American and Australian lizard faunas. To enable exponents to be calculated as accurately as possible animals covering a wide mass range, both within and between species, were obtained. However, most of the work concentrated on reptiles weighing less than 1 kg, since most of the mammals used in the study were also within this size range. The approach used was to determine first the relationships between metabolism and body mass individually for each species. This enables it to be established whether any differences in metabolic levels or exponents exist between species before attempting to combine data and make generalisations about the relationships in larger taxonomic groups.

2.2 MATERIALS AND METHODS

2.2.1 Animals

Sources

The reptiles were imported directly, by air, from Egypt and Kuwait or purchased from various commercial suppliers. A full list of the species, and numbers of each used, is given in Table 2.1.

Maintenance

Lizards were kept in plastic, glass or stainless steel tanks ranging in size from 34 x 24 x 20 cm for the smaller species, to 100 x 50 x 50 cm for larger individuals. The tanks contained a 2 to 6 cm deep gravel substrate, on which were arranged rocks and pieces of wood to provide suitable retreats for the animals. A deep peat and sand substrate was used instead of gravel for the temperate fossorial species *Anguis fragilis* and *Chalcides chalcides*. Smaller species were kept in groups of up to fifteen animals, while large more aggressive lizards, such as varanids, were normally housed individually. The crocodilians were kept in large plastic or stainless steel tanks containing about 10 to 15 cm of water and large rocks onto which they could haul out.

All tanks were located in a quiet well ventilated room, the temperature and photoperiod of which could be accurately regulated. The temperature of the room was kept at 30°C, with no additional radiant heat sources available to the reptiles. A 12 L:12 D photoperiod was maintained, the photophase commencing at 08.00 GMT. Illumination was provided by Truelite fluorescent tubes (Xenopus Ltd.) which have the advantage of emitting radiation containing the shorter wavelengths beneficial to reptiles under captive conditions while

Table 2.1 Species and quantities of reptiles used during the present study

Family	Species		n
Sauria			
Lacertidae	Lacerta (Podarcis) sicula	Italian wall lizard	10
	Lacerta (Podarcis) muralis	Common wall lizard	8
	Lacerta (Podarcis) lilfordi	Lilford's wall lizard (melanistic phase)	20+
	Lacerta vivipara	Viviparous lizard	20+
	Lacerta viridis	Green lizard	20+
	Lacerta lepida	Ocellated lizard	3
Cordylidae	Cordylus jonesi	Jones' zonure	50+
	Cordylus vittifer	Red zonure	8
	Cordylus warreni	Warren's zonure	4
	Cordylus giganteus	Giant zonure	6
Scincidae	Scincus scincus	Sand skink	8
	Chalcides chalcides	Three-toed skink	3
	Chalcides ocellatus	Ocellated skink	14
Gekkonidae	Tarentola mauritanica	Moorish gecko	10
Agamidae	Agama stellio	Starred agama	8
Chamaeleonidae	Chamaeleo chamaeleon	Common chamaeleon	5
Anguidae	Anguis fragilis	Slow-worm	5

Table 2.1 continued

Family	Species		n
Varanidae	Varanus griseus	Grey monitor	3
	Varanus exanthmaticus	Savannah monitor	3
Crocodilia			
Crocodylidae	Caiman sclerops	Spectacled caiman	8

producing very little radiant heat.

The smaller lizards were fed on a diet of live insects, consisting predominantly of *Locusta* hoppers and larval and adult *Tenebrio*. Larger species were given adult locusts and young or adult mice, according to their size. All reptiles had continuous access to fresh drinking water. Only animals which had adjusted to captive conditions and were feeding freely were used in experiments.

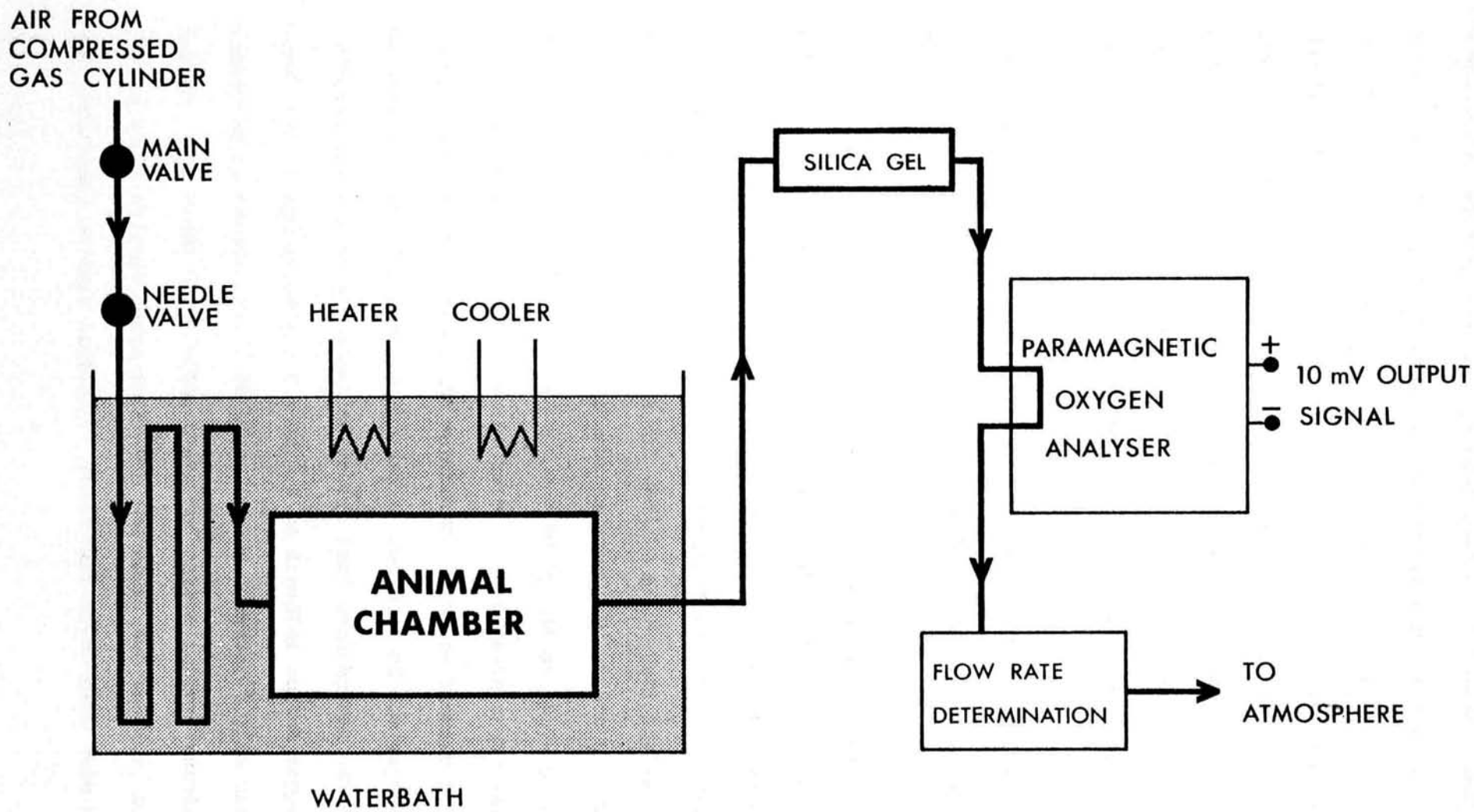
2.2.2 Determination of standard metabolic rate (SMR)

Metabolic rates were determined using indirect calorimetry, by measuring the rates of oxygen consumption of animals in an open flow-through system (Fig. 2.1). During experiments the unrestrained reptile was enclosed within a chamber, through which a moving stream of air was continually passed. Different chambers were used, as appropriate for the size of each animal. The relative size of the chamber was kept small both to reduce unwanted locomotory activity and minimise the dead volume, and therefore the response time, of the system. The smaller chambers, from approximately 20 to 200 ml were made from glass tubing of various diameters. When in use these were closed at each end with rubber stoppers, through which short lengths of 0.5 cm diameter glass tubing were fitted to carry the incoming and effluent gases. Larger chambers, up to a capacity of 10 litres, were constructed from 0.5 cm thick sheet perspex. These had separate lids held in place by brass screws and sealed, during immersion, with vaseline and rubber washers.

The temperature of these chambers was regulated by submerging them in large thermostatically controlled water baths. Each of these was heated by two electric immersion heaters and cooled, when required, by an external cooling unit controlled by a mercury contact thermostat.

Figure 2.1 Schematic diagram of the open circuit apparatus used to determine the standard metabolic rates of both reptiles and mammals by measuring their oxygen consumption.

Fig. 2.1


AIR FROM COMPRESSED GAS CYLINDER
MAIN VALVE
NEEDLE VALVE
HEATER
COOLER
ANIMAL CHAMBER
WATERBATH
SILICA GEL
PARAMAGNETIC OXYGEN ANALYSER
+
10 mV OUTPUT
−
SIGNAL
FLOW RATE DETERMINATION
TO ATMOSPHERE

A mechanical stirrer was used to ensure adequate thermal mixing of the water in the bath. The system held the water temperature to an accuracy of ± 0.1°C at all temperatures in the range 4 to 37°C. The high heat capacity and thermal conductivity of water enabled the temperature of the chamber to be regulated much more precisely than if it had been surrounded by air. It also had the advantages of making any gas leaks in the system, which would cause inaccuracies in the results, immediately obvious and helped to isolate the animals from visual and noise disturbance. Two stainless steel waterbaths were used. The smaller, measuring 80 x 50 x 30 cm and holding approximately 100 litres, was used for the majority of the work while the larger, measuring 140 x 50 x 35 cm with a capacity of 210 litres, was used for larger reptiles such as varanids and crocodilians. Two experimental chambers, and associated equipment, could be used simultaneously with each waterbath.

Dry air was passed through each chamber from a compressed gas cylinder. In addition to the high pressure valves on the cylinder heads a secondary needle valve was used to allow very precise control of the rate of air flow through the chamber. To ensure that the interiors of the chambers were not cooled by the air flowing through them, considerable care had to be taken to ensure this gas was brought to the same temperature as the waterbath. The low thermal conductivity of air, and the high flow rates used in the some of the experiments, required the use of extremely effective heat exchangers. Each consisted of approximately 8 m of 0.8 cm diameter coiled copper tubing connected in series with a further 20 m of narrower 0.3 cm diameter tubing. The wider bore tubing contained coarse copper turnings to increase the area of contact between the metal and the air, improving the efficiency of heat transfer. These heat exchangers were mounted

in the same waterbaths as the chambers to which they were connected. For the highest flow rates used supplementary heating could be applied by first passing the air through a small stainless steel box, packed with metal turnings, heated by gas burners before it entered the submerged heat exchangers. Each experimental chamber was mounted in series with its own individual heat exchanger. The effectiveness of the heat exchangers, across the range of temperatures and flow rates used in the experiments, was checked by mounting a thermistor inside the chamber to confirm that the air temperature was always isothermal with the waterbath.

After passing through a tube of silica gel to remove water vapour expired by the animal, the oxygen concentration of the effluent gas from each chamber was measured using a Taylor-Servomex OA.272 paramagnetic gas analyser. Immediately prior to the introduction of experimental animals into the chambers these analysers were calibrated with pure nitrogen to set the zero, and air to set full scale deflection. During experiments the analysers were set to their range of maximum sensitivity for oxygen concentrations in the range of 16 to 21%, and the results continually displayed as a 0 to 10 mV signal on potentiometric recorders. Immediately after every experiment all analysers were re-calibrated and if the baseline drift had exceeded 2.5% of full scale deflection the results were disregarded. Drifts of less than this were assumed to be linear and the oxygen concentration calculated accordingly.

The flow rate of gas through the system was measured using collection by the downward displacement of water. This method allowed a more accurate determination of the lower flow rates than would have been achieved with a flowmeter. All values were corrected for the

vapour pressure of water at room temperature. To ensure the reptile was maintained in a near normal gaseous environment a flow rate was used which prevented the oxygen concentration in the chamber from falling below 20% while the animal was at rest. These flow rates were varied according to the size of the reptile and the temperature at which the experiment was being conducted, and ranged from less than 5 ml/min, for smaller lizards, to in excess of 150 ml/min for varanids and crocodilians. To check that the flow rate of gas through each chamber remained stable it was monitored several times during the course of every experiment.

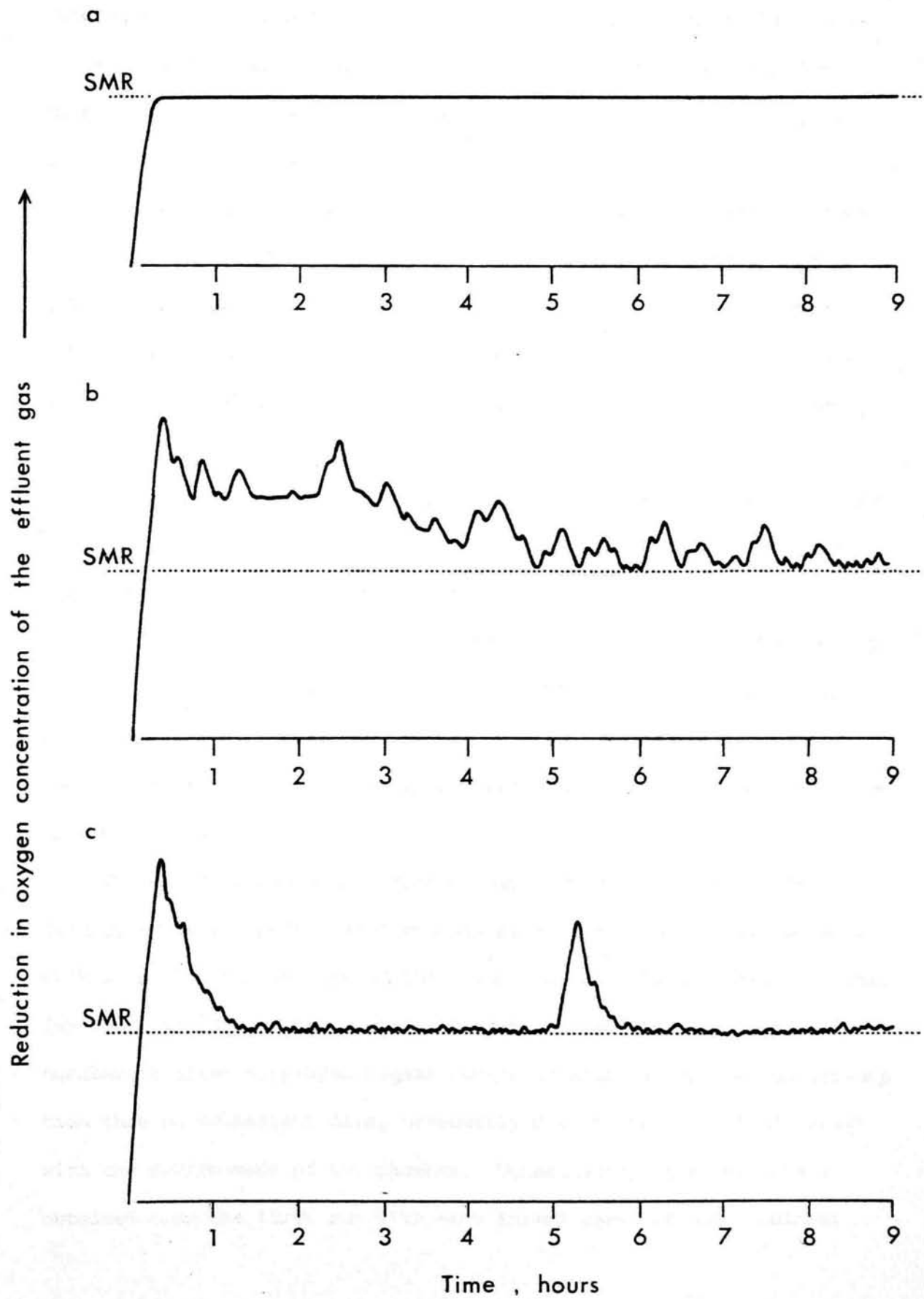
Calculations for determining the oxygen consumption of the animal, from the flow rate through the chamber and the difference in oxygen concentration between the gas entering and leaving it, were based on the formulae of Depocas & Hart (1957). All gaseous volumes were converted to standard temperature and pressure (273°K at 760mm of mercury). An additional consideration is that because the respiratory quotients (RQ) of the animals will be less than unity, the total volume of gas leaving the chamber will be slightly less than that entering it. Although this will introduce an insignificant error into the determinations of flow rate, it will result in the measurements of oxygen concentration in the effluent gas appearing artificially high. These were therefore corrected using an RQ of 0.7, a value typical of resting and fasting squamate reptiles (Potter & Glass, 1931; Kramer, 1934; Cook, 1949; Roberts, 1968). Since deviations from this RQ of up to 0.1 will only result in errors in the calculated oxygen consumption rate of 2%, it was considered acceptable to use this assumed value rather than undertake determinations of carbon dioxide production during every experiment.

Another problem is deciding which features of the trace actually represent the animals' resting metabolic rate. Ideally the metabolism of the animal would be constant throughout the experiment, and therefore the reduction in oxygen concentration measured would be the same (Fig. 2.2a). However, preliminary experiments had shown that the oxygen concentration of the effluent gas from the chamber varied considerably throughout the measurement period. This was because not only resting metabolism but elevations caused by activity of the animal were being monitored. Usually after introducing a reptile into the apparatus there is an initial rise in metabolic rate until the animal settles into the chamber. This period may last several hours, demonstrating the need for long measurement periods when determining reptilian metabolic rates. Sometimes oxygen consumption subsequently settled to a virtually constant level for the remainder of the experiment. However, more often periodic elevations continued, which could usually be correlated with activity of the animal in the chamber. Between these peaks the traces usually returned to the same minimum level, which was taken as corresponding to resting metabolic rate. This was often confirmed by longer periods of stable oxygen consumption, at the same low level, later in the experiment. Two sample reptilian traces and the levels interpreted as representing reptilian metabolism are shown in Fig. 2.2. The values quoted throughout this study are not therefore the mean rates of total oxygen consumption during an experiment, but relate specifically to resting metabolic rate. Determinations made using other techniques, such as manometry, which measure cumulative oxygen consumption may include some of those elevations due to activity and will therefore tend to overestimate resting metabolism.

Figure 2.2 (a) Hypothetical trace of an animal consuming oxygen at a constant rate throughout the measurement period.

(b) & (c) Examples of traces obtained from small lizards during actual experiments. The levels of oxygen consumption taken as representing standard metabolic rate are indicated with broken lines.

Fig. 2.2


a
SMR
1
2
3
4
5
6
7
8
9
b
SMR
1
2
3
4
5
6
7
8
9
c
SMR
1
2
3
4
5
6
7
8
9
Reduction in oxygen concentration of the effluent gas
Time , hours

2.2.3 Experimental Procedures

After arrival in the laboratory all reptiles were acclimated to 30°C on a 12 L:12 D photoperiod, under the conditions described above, for a minimum period of six weeks before being used in experiments. In practice animals were usually kept for longer than this, in some instances in excess of a year.

Measurements of resting metabolic rate require the reptile to be in a post-absorptive state, since while food is being assimilated metabolism is elevated above its normal level (Coulson & Hernandez, 1980). Consequently, all food was withheld for the five days before determinations of oxygen consumption were made. During this fasting period drinking water was still freely available.

For measurements animals were removed from their holding tanks and introduced into the apparatus soon after the start of the photophase. Recordings of oxygen consumption were made until suitable traces of resting metabolism were obtained. The minimum experimental period was 8 hours, with the reptile not normally being kept in the chamber for more than 15 hours. The mass of the reptile was measured immediately before and after being placed in the apparatus, and the mean value used in the calculations.

The oxygen consumption rates of each individual lizard were determined over a period of five consecutive days; the first two days with a chamber temperature of 30°C, two runs at 37°C and then the final day again at 30°C. The first occasion an animal was placed in the chamber it often displayed higher levels of activity and oxygen consumption than on subsequent days, presumably due to initial unfamiliarity with the environment of the chamber. Consequently, the recordings obtained from the first run with each animal were not used, neither

were any on subsequent days if the animal refused to settle. Between experiments the lizards were returned to their holding tanks and maintained under normal conditions, although food was still withheld. The procedure with crocodilians was exactly the same except the experiments were conducted at chamber temperatures of 25 and 30°C.

2.2.4 Statistical analysis of results

Exponents, b, relating SMR to body mass were only produced for groups of animals from which a minimum of 8 determinations had been made, covering a mass range in which the largest and smallest individuals differed by a factor of two. Values were calculated by linear regression of logarithmically transformed data (see Chapter 1.3). Since the errors associated with measurements of body mass (the abscissa) are considered to be negligible, least squares regression was used. Mean SMRs were calculated for species from which less extensive data were obtained. Students t-test was used for statistical comparisons between groups of data. In all cases probabilities of < 0.05 were accepted as indicating significance.

2.3 RESULTS AND DISCUSSION

2.3.1 Determinations of standard metabolic rate (SMR)

The SMRs of a total of 19 lizard species were determined at 30°C. Sufficient measurements were obtained from 11 species to enable the relationship between SMR and body mass to be examined. The data for these species are presented graphically in Figs. 2.3 to 2.13, and the linear regression parameters are summarised in Table 2.2. The mean SMRs of the other 9 species, from which less data were obtained, are presented in Table 2.3.

More than one species were examined from each of the three genera *Lacerta*, *Cordylus* and *Varanus*. Intra-generic exponents were calculated for these three genera by regressing together all the individual SMR measurements of their member species (Figs.2.14 to 2.18, Table 2.4). No attempt was made to calculate a composite exponent for *Scincus*, since the two species of this genus examined clearly possessed different metabolic levels (see 2.3.3).

The oxygen consumption rates of species known to possess relatively low preferred body temperatures (see Chapter 6.3), such as gekkonids, chamaeleonids and anguids, were not measured at 37°C. It was also decided not to risk any large cordylids after two *Cordylus warreni* died in the chamber during exposure to this higher temperature. This was unexpected, as it was assumed that 37°C would be within the tolerance range of these tropical African lizards. Therefore, only a total of 14 lizard species had their SMRs measured at 37°C. Of these suitable data were obtained from 8 species for the exponents relating their SMRs to body mass to be calculated (Figs. 2.19 to 2.26, Table 2.5). The mean SMRs of the remaining 6 species are given in Table 2.3. Sufficient data were available at 37°C to allow only a single intra-

Table 2.2 Regression parameters of the relationship between standard metabolic rate (SMR) and body mass for lizards at 30° C

Species	n	Body mass, g range (mean)	Intercept, a	Exponent, b, ± 95% confidence limits Total (Mass specific)	r
Lacerta sicula	20	3.2-9.1 (6.6)	0.189	0.81 ± 0.16* (-0.19 ± 0.16*)	0.93
Lacerta viridis	29	11.2-37.8 (23.4)	0.216	0.78 ± 0.19* (-0.22 ± 0.19*)	0.85
Cordylus jonesi	36	3.7-16.9 (11.7)	0.093	0.86 ± 0.09* (-0.14 ± 0.09*)	0.96
Cordylus vittifer	9	7.6-17.1 (12.8)	0.129	0.75 ± 0.33* (-0.25 ± 0.33)	0.90
Cordylus giganteus	15	14.0-214 (70.8)	0.150	0.76 ± 0.11* (-0.24 ± 0.11*)	0.97

*$p < 0.05$

Table 2.2 continued

Species	n	Body mass, g range (mean)	Intercept, a	Exponent, b, ± 95% confidence limits Total (Mass specific)	r
Scincus scincus	17	9.6-28.3 (19.1)	0.165	0.81 ± 0.22* (-0.19 ± 0.22)	0.90
Chalcides ocellatus	22	8.2-34.4 (20.1)	0.137	0.81 ± 0.17* (-0.19 ± 0.17*)	0.91
Tarentola mauritanica	12	7.2-33.2 (21.2)	0.087	0.88 ± 0.15* (-0.12 ± 0.15)	0.97
Agama stellio	10	27.2-54.6 (39.5)	0.167	0.88 ± 0.47 (-0.12 ± 0.47)	0.83
Chamaeleo chamaeleon	8	16.5-40.8 (28.1)	0.389	0.68 ± 0.39* (-0.32 ± 0.39)	0.87
Anguis fragilis	10	3.7-14.4 (7.5)	0.253	0.76 ± 0.14* (-0.24 ± 0.14*)	0.98

Figures 2.3-2.13 Relationships of (a) total and (b) mass specific standard metabolic rate to body mass for lizards at 30°C. Heavy lines were fitted by linear regression analysis. The outer pair of lines represent the 95% confidence limits for predicted values of standard metabolic rate.

Figure 2.3 *Lacerta sicula*

Figure 2.4 *Lacerta viridis*

Figure 2.5 *Cordylus jonesi*

Figure 2.6 *Cordylus vittifer*

Figure 2.7 *Cordylus giganteus*

Figure 2.8 *Scincus scincus*

Figure 2.9 *Chalcides ocellatus*

Figure 2.10 *Agama stellio*

Figure 2.11 *Chamaeleo chamaeleon*

Figure 2.12 *Tarentola mauritanica*

Figure 2.13 *Anguis fragilis*

Fig. 2.3

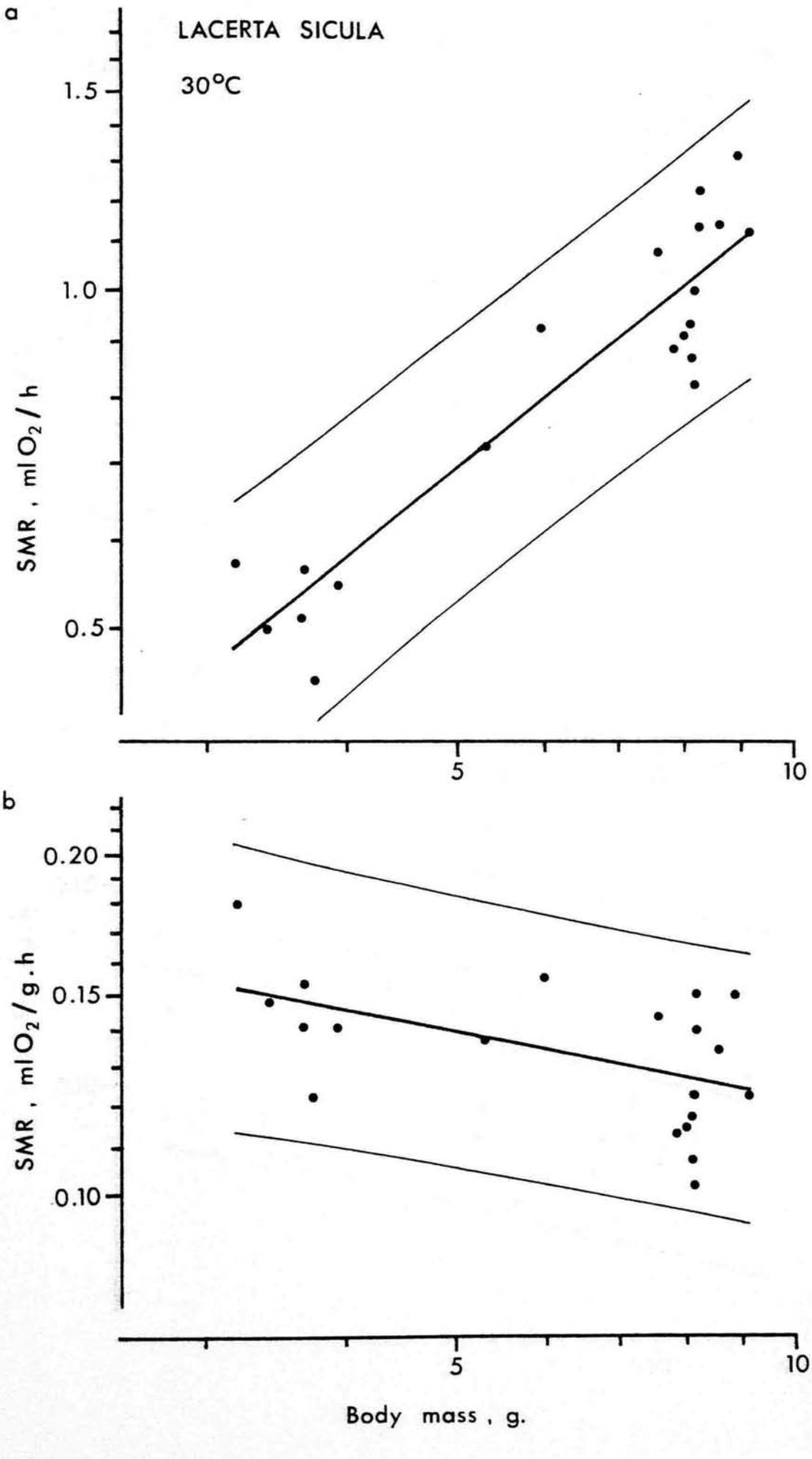

a
LACERTA SICULA
30°C
1.5
1.0
0.5
SMR , ml O_2 / h
5
10
b
0.20
0.15
0.10
SMR , ml O_2 / g.h
5
10
Body mass , g.

Fig. 2.4

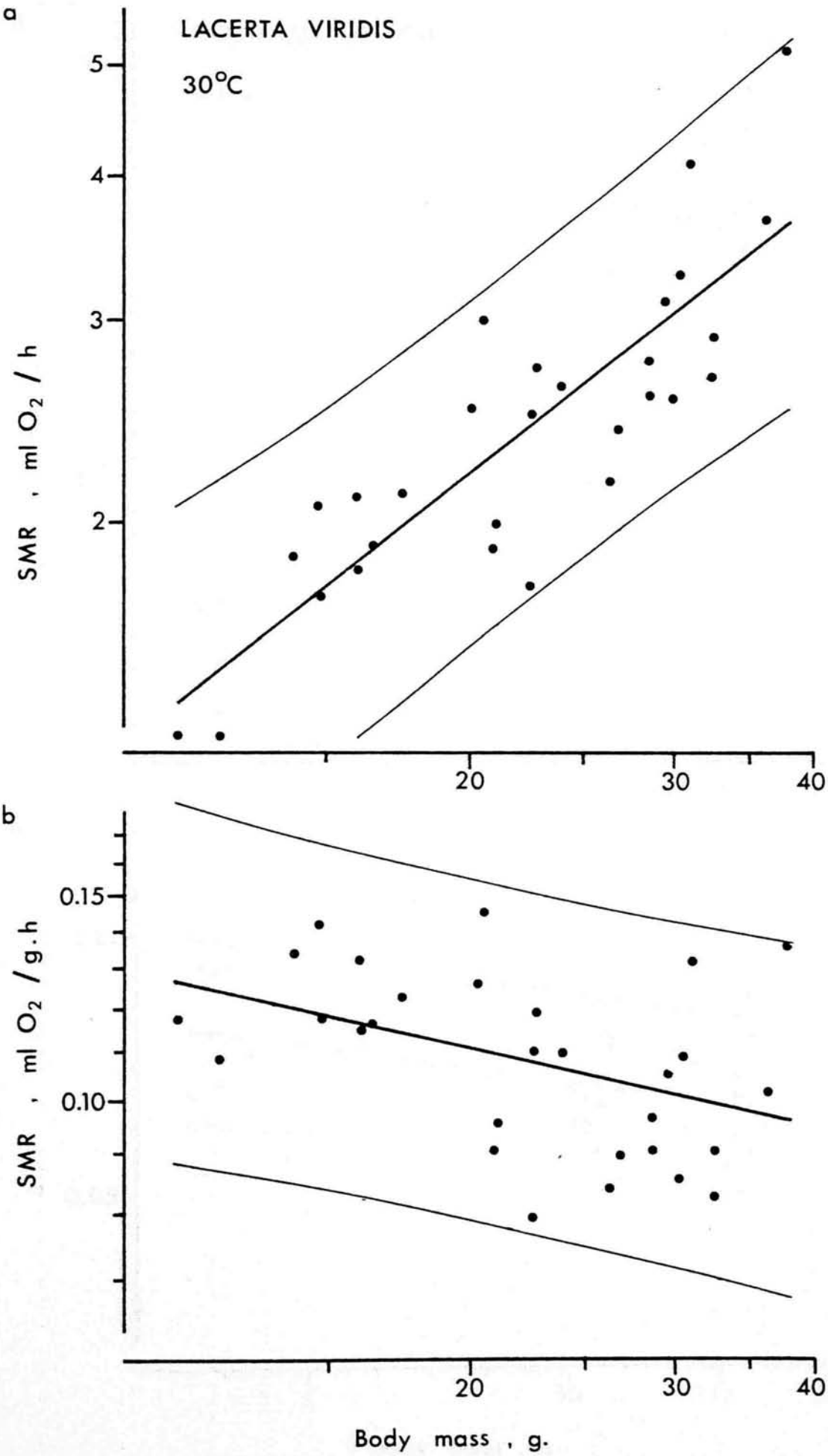

a
LACERTA VIRIDIS
30°C
5
4
3
2
SMR , ml O_2 / h
20
30
40
b
0.15
0.10
SMR , ml O_2 /g.h
20
30
40
Body mass , g.

Fig. 2.5

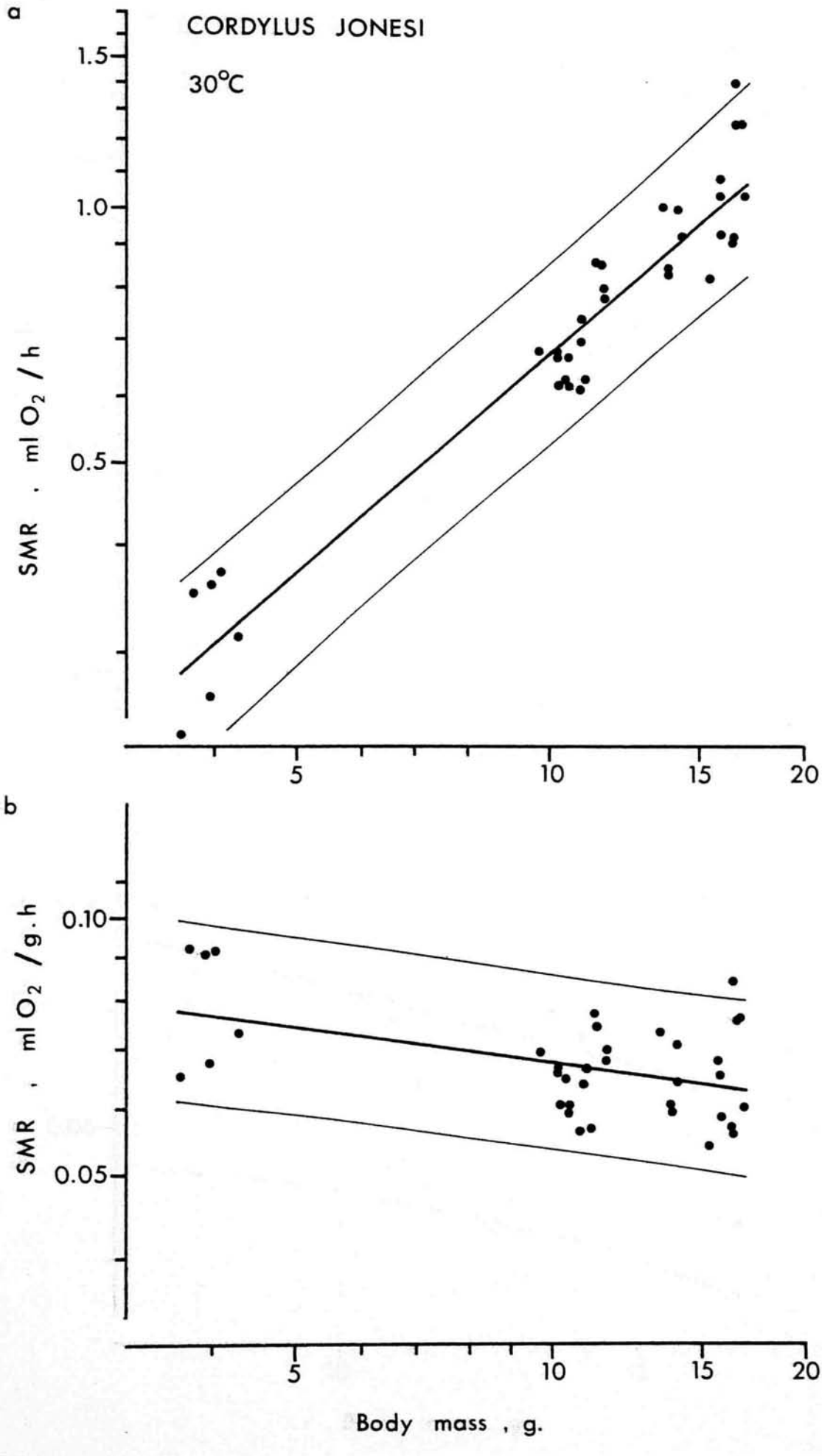

a
CORDYLUS JONESI
30°C
1.5
1.0
0.5
SMR , ml O_2 / h
5
10
15
20
b
0.10
0.05
SMR , ml O_2 /g.h
5
10
15
20
Body mass , g.

Fig. 2.6

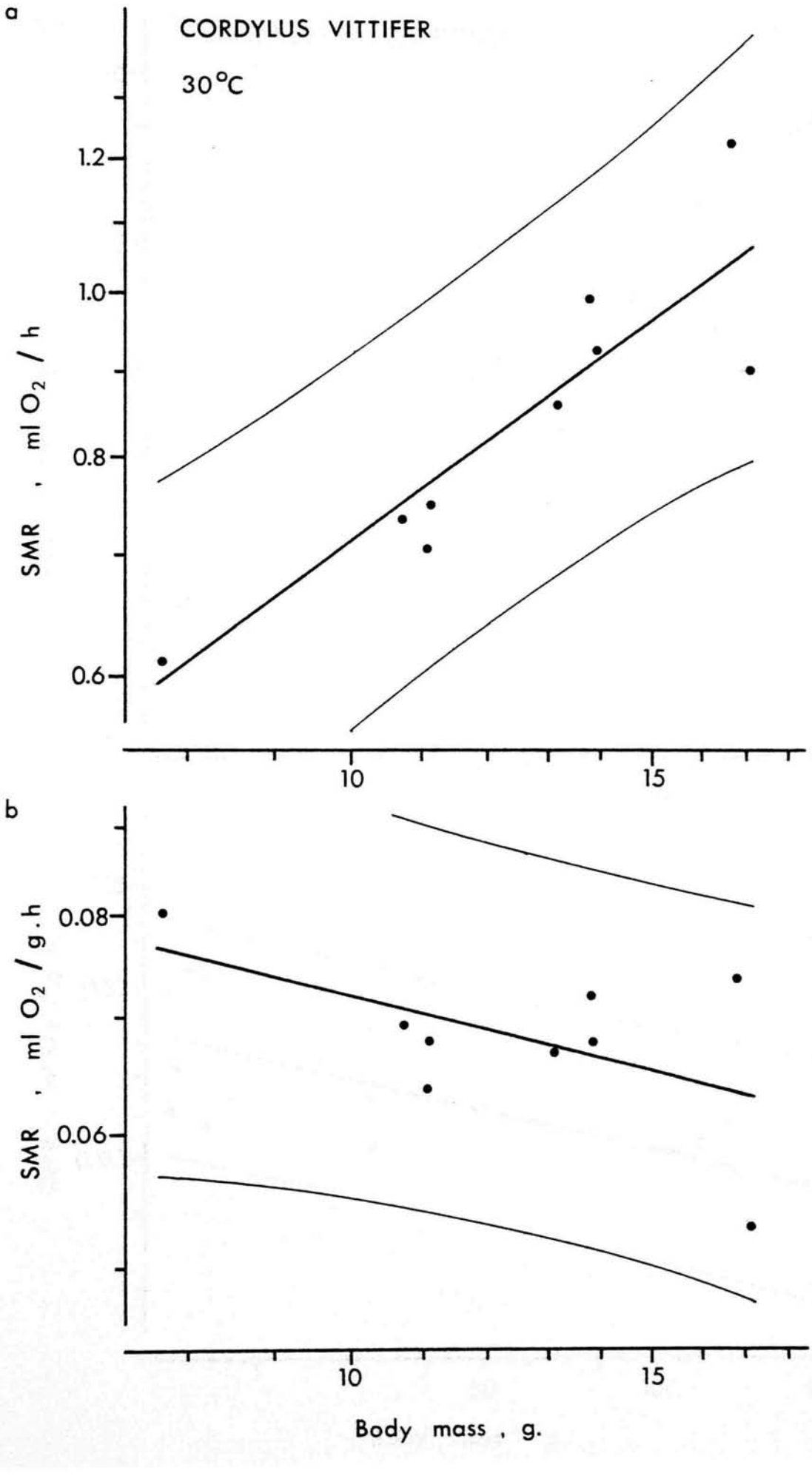

a
CORDYLUS VITTIFER
30°C
1.2
1.0
0.8
0.6
SMR , ml O_2 / h
10
15
b
0.08
0.06
SMR , ml O_2 / g.h
10
15
Body mass , g.

Fig. 2.7

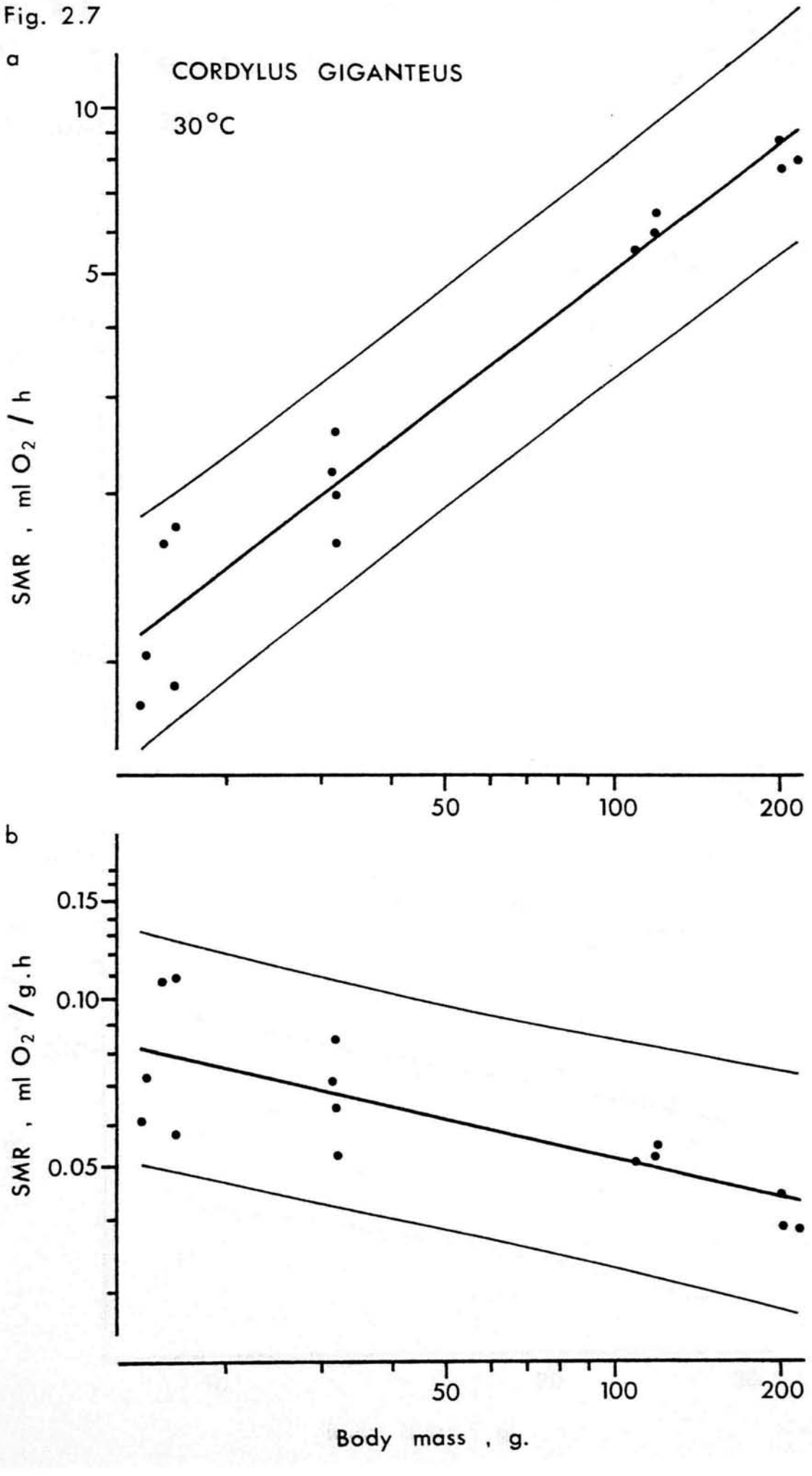

a
CORDYLUS GIGANTEUS
30 °C
10
5
SMR , ml O2 / h
50
100
200
b
0.15
0.10
0.05
SMR , ml O2 / g.h
50
100
200
Body mass , g.

Fig. 2.8

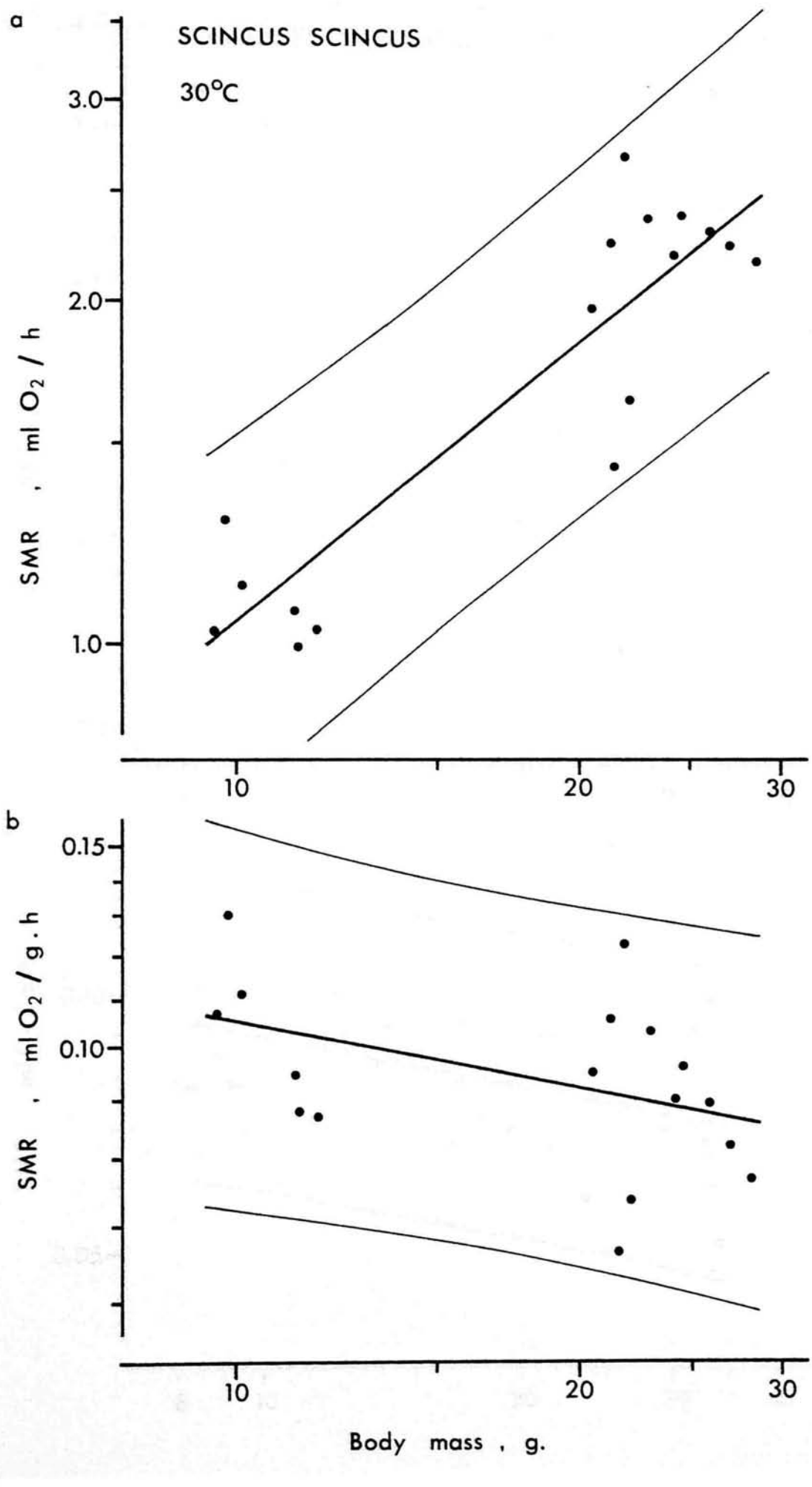

a
SCINCUS SCINCUS
30°C
3.0
2.0
1.0
SMR , ml O_2 / h
10
20
30
b
0.15
0.10
SMR , ml O_2 / g . h
10
20
30
Body mass , g.

Fig. 2.9

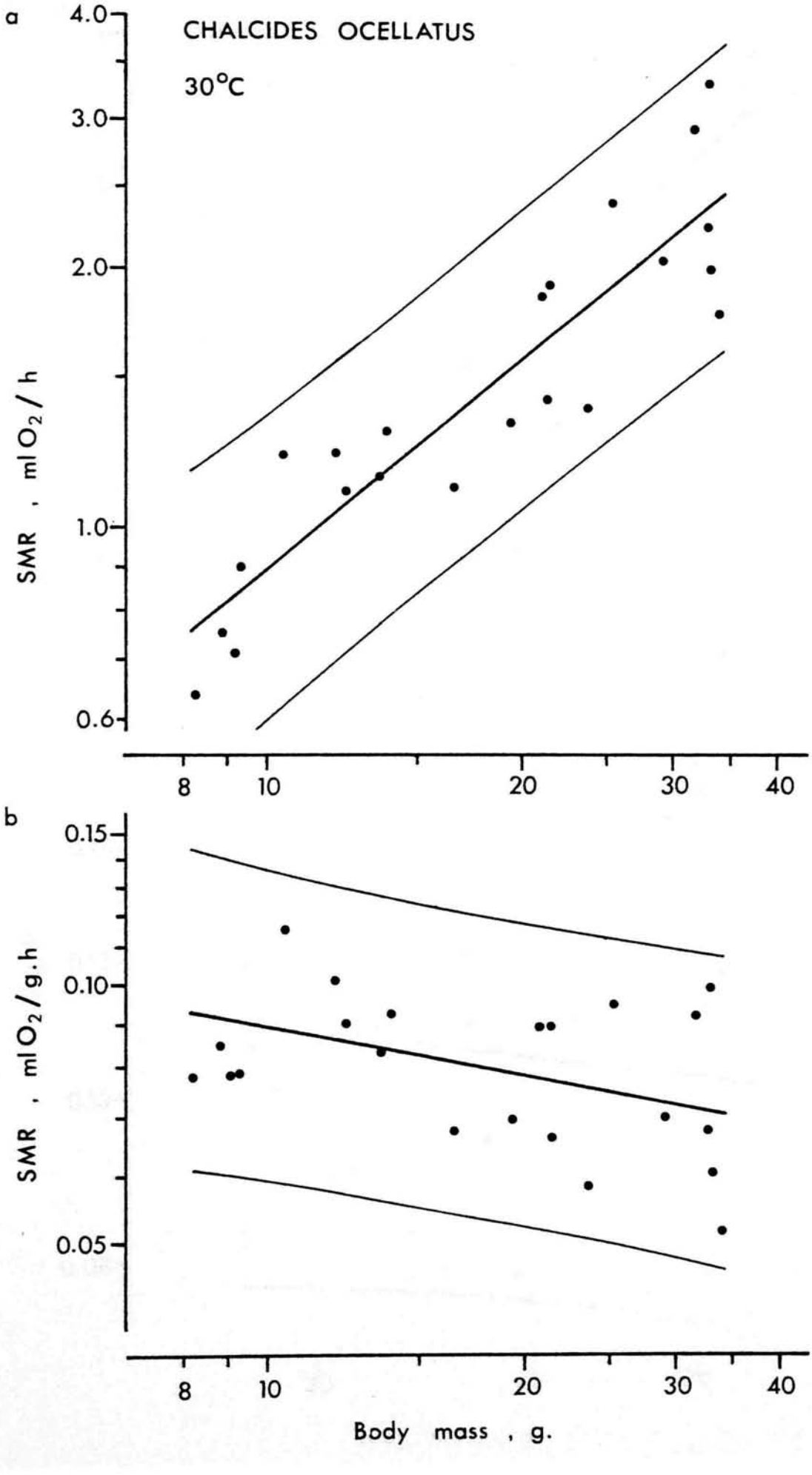

a
CHALCIDES OCELLATUS
30°C
4.0
3.0
2.0
1.0
0.6
SMR , ml O2 / h
8
10
20
30
40
b
0.15
0.10
0.05
SMR , ml O2 / g.h
8
10
20
30
40
Body mass , g.

Fig. 2.10

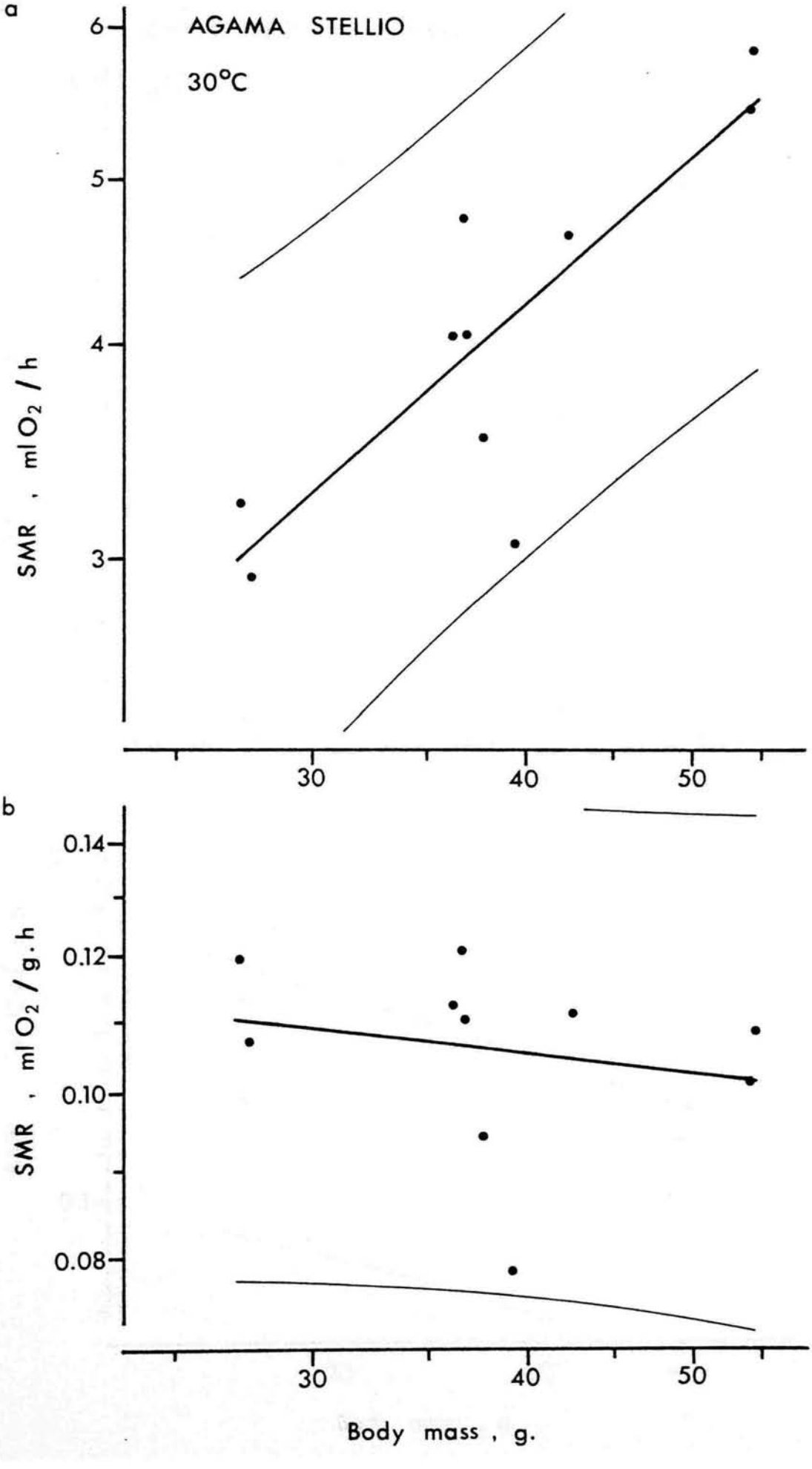

a
AGAMA STELLIO
30°C
6
5
4
3
SMR , ml O_2 / h
30
40
50
b
0.14
0.12
0.10
0.08
SMR , ml O_2 / g.h
30
40
50
Body mass , g.

Fig. 2.11

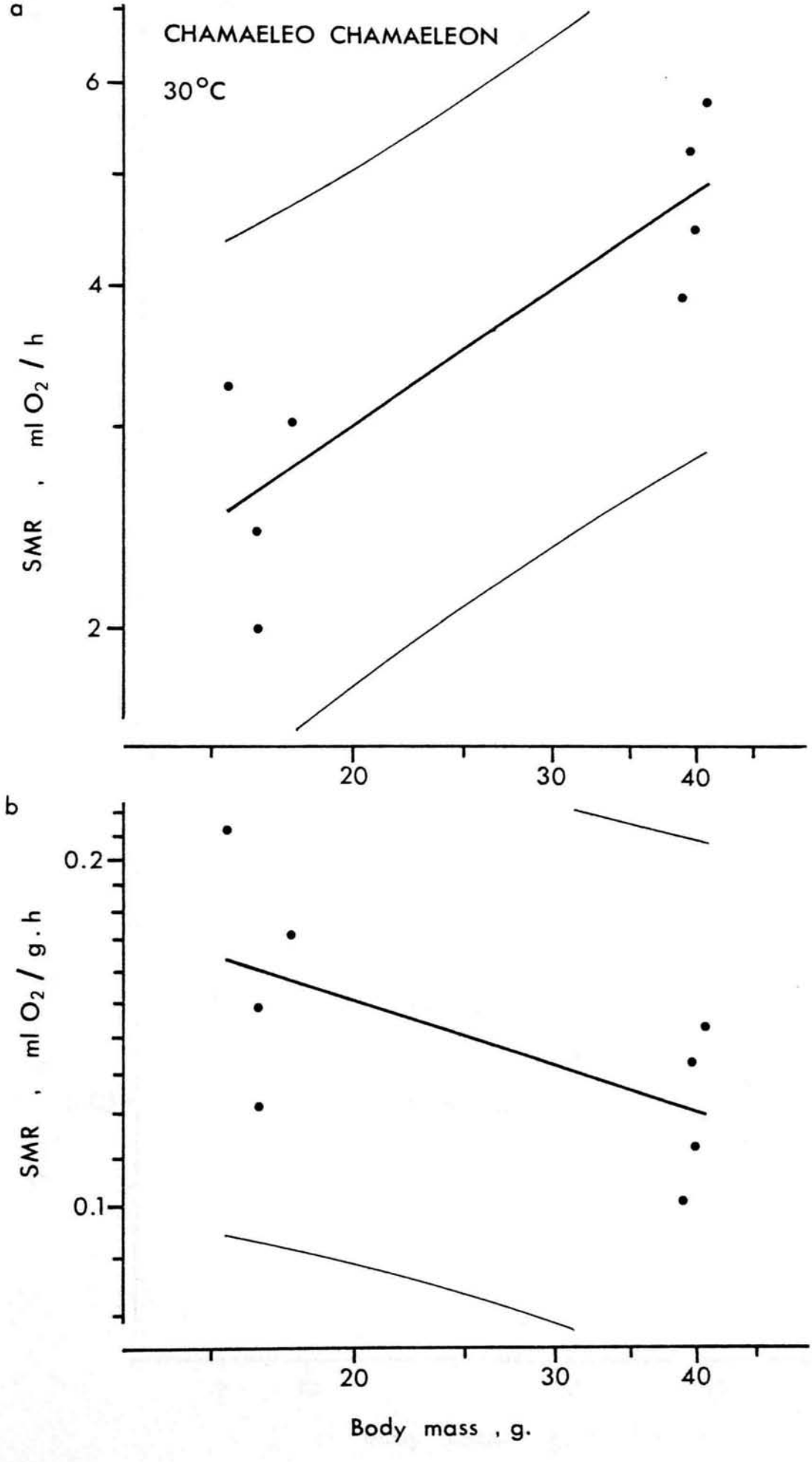

a
CHAMAELEO CHAMAELEON
30°C
6
4
2
SMR , ml O_2 / h
20
30
40
b
0.2
0.1
SMR , ml O_2 / g . h
20
30
40
Body mass , g.

Fig. 2.12

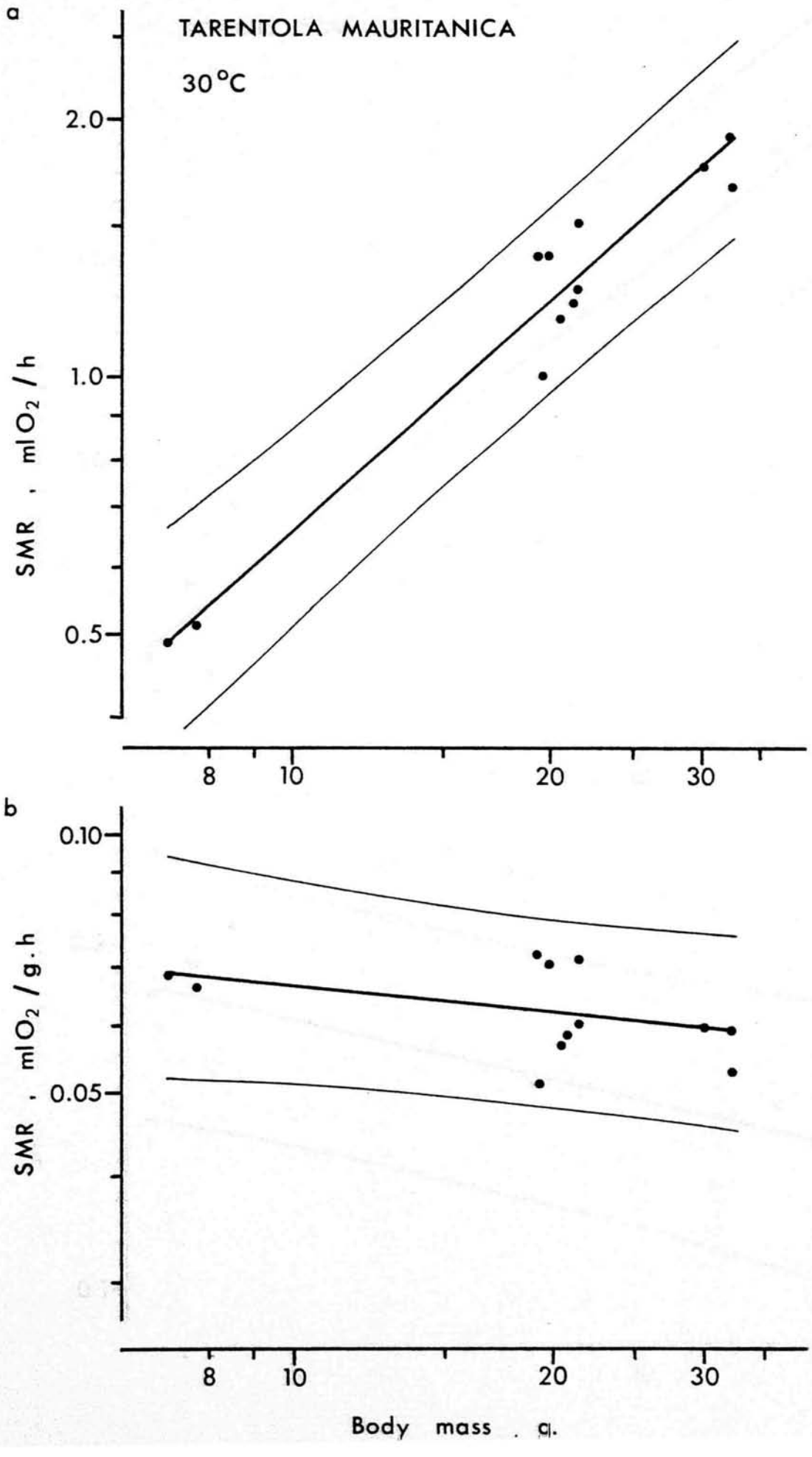

a
TARENTOLA MAURITANICA
30°C
2.0
1.0
0.5
SMR . ml O2 / h
8
10
20
30
b
0.10
0.05
SMR . ml O2 / g.h
8
10
20
30
Body mass . g.

Fig. 2.13

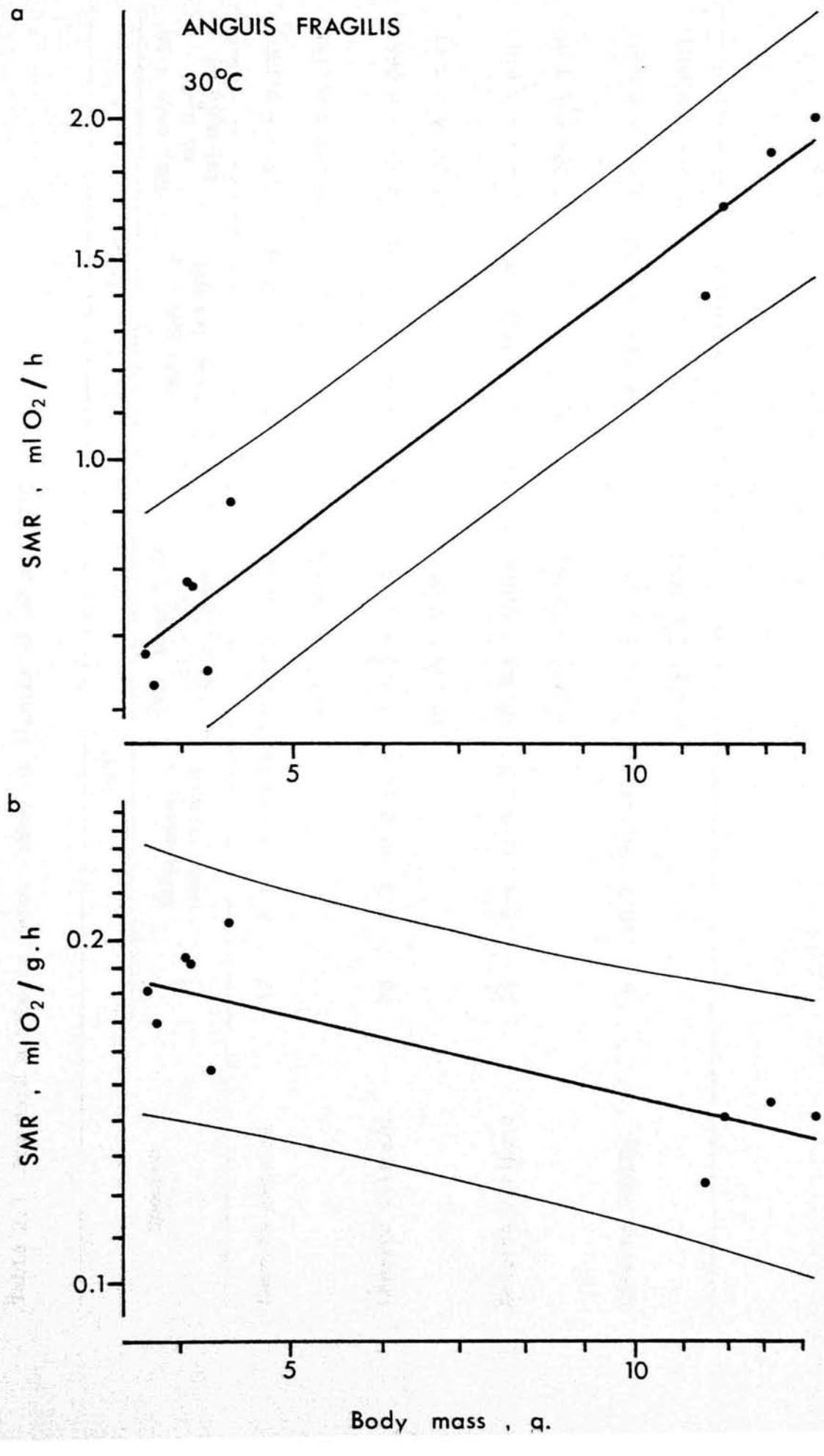

a
ANGUIS FRAGILIS
30°C
2.0
1.5
1.0
SMR , ml O2 / h
5
10
b
0.2
0.1
SMR , ml O2 / g.h
5
10
Body mass , g.

Table 2.3 Standard metabolic rates (SMRs) of lizards at 30 and 37°C

Species	30°C			37°C		
	n	Body mass, g mean (range)	SMR, mean ± SE ml O_2/h ($ml\ O_2$/g.h)	n	Body mass, g mean (range)	SMR, mean ± SE ml O_2/h ($ml\ O_2$/g.h)
Lacerta muralis	12	6.7 (4.6-8.2)	0.824 ± 0.044 (0.127 ± 0.010)	14	6.1 (3.5-8.2)	1.519 ± 0.100 (0.260 ± 0.014)
Lacerta lilfordi	28	9.8 (8.0-11.9)	1.162 ± 0.045 (0.118 ± 0.003)	15	9.9 (8.0-12.1)	2.095 ± 0.061 (0.215 ± 0.009)
Lacerta vivipara	14	2.4 (1.9-2.9)	0.364 ± 0.015 (0.153 ± 0.006)	11	2.3 (1.9-2.9)	0.679 ± 0.040 (0.298 ± 0.015)
Lacerta lepida	6	28.9 (20.7-37.0)	3.261 ± 0.306 (0.117 ± 0.005)	7	24.6 (17.5-34.5)	4.883 ± 0.651 (0.198 ± 0.005)

Table 2.3 continued

Species	30°C			37°C		
	n	Body mass, g mean (range)	SMR, mean ± SE ml O_2/h ($ml\ O_2$/g.h)	n	Body mass, g mean (range)	SMR, mean ± SE ml O_2/h ($ml\ O_2$/g.h)
Cordylus warreni	8	47.6 (31.3-54.0)	2.847 ± 0.143 (0.061 ± 0.003)			
Chalcides chalcides	6	9.7 (6.4-13.2)	1.498 ± 0.258 (0.153 ± 0.007)	6	9.5 (6.4-12.6)	2.271 ± 0.347 (0.239 ± 0.010)
Varanus griseus	5	443 (206-600)	22.965 ± 3.455 (0.056 ± 0.005)	3	301 (214-470)	36.298 ± 8.042 (0.124 ± 0.008)
Varanus exanthmaticus	6	668 (465-870)	35.700 ± 4.238 (0.054 ± 0.002)			

Table 2.4 Regression parameters of the overall relationship between standard metabolic rate (SMR) and body mass within lizard genera

Genus	Temperature, °C	Number of species	n	Body mass, g range (mean)	Intercept, a	Exponent, b, ± 95% confidence limits Total (Mass specific)	r
Lacerta	30	6	109	1.9-37.7 (12.6)	0.170	0.85 ± 0.04* (-0.15 ± 0.04*)	0.97
	37	6	99	1.9-37.2 (12.9)	0.352	0.80 ± 0.03* (-0.20 ± 0.03*)	0.98
Cordylus	30	4	68	3.7-214 (29.1)	0.096	0.86 ± 0.04* (-0.14 ± 0.04*)	0.98
Varanus	30	2	11	206-870 (566)	0.222	0.79 ± 0.168 (-0.21 ± -.168*)	0.96

*$p < 0.05$.

Figure 2.14 Relationship of total standard metabolic rate to body mass for lizards of the genus *Lacerta* at 30°C.

Figure 2.15 Relationship of mass specific metabolic rate to body mass for lizards of the genus *Lacerta* at 30°C. For key see Fig. 2.14.

Fig. 2.14

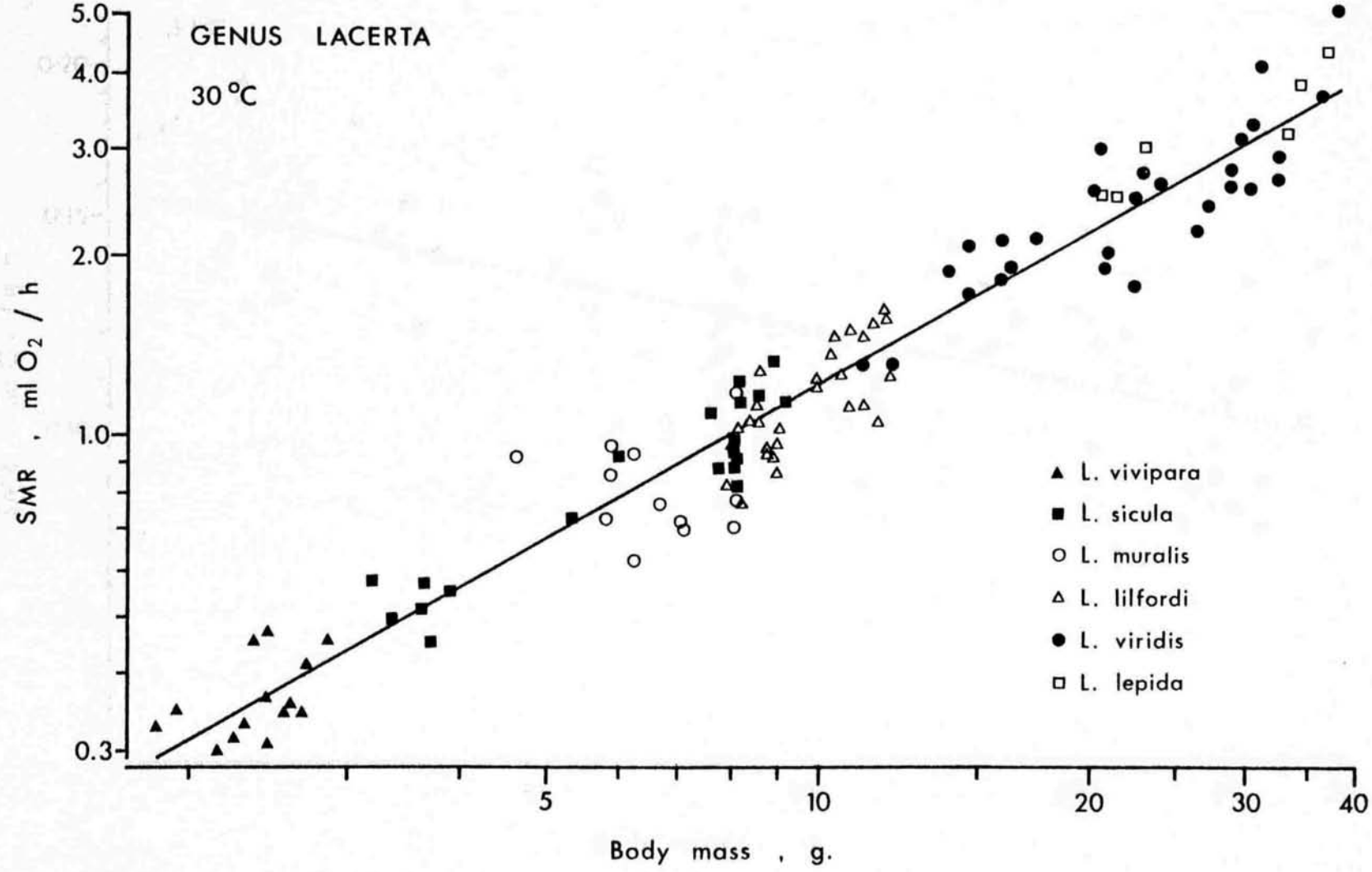

GENUS LACERTA
30 °C
SMR . ml O_2 / h
5.0
4.0
3.0
2.0
1.0
0.3
5
10
20
30
40
Body mass , g.
L. vivipara
L. sicula
L. muralis
L. lilfordi
L. viridis
L. lepida

Fig. 2.15 GENUS LACERTA

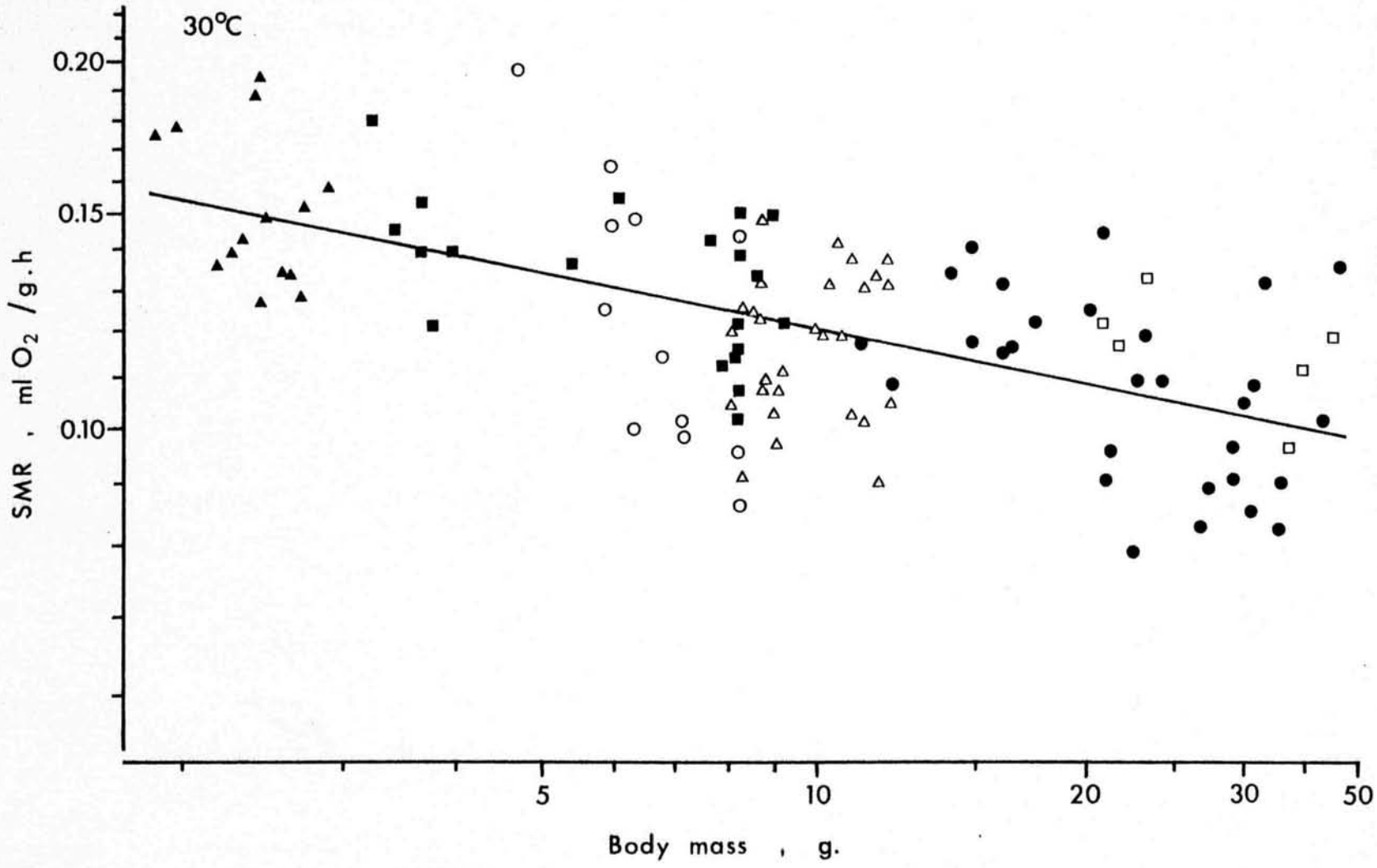


Figure 2.16 Relationship of total standard metabolic rate to body mass for lizards of the genus *Cordylus* at 30°C.

Figure 2.17 Relationship of mass specific standard metabolic rate to body mass for lizards of the genus *Cordylus* at 30°C. For key see Fig. 2.16.

Fig. 2.16

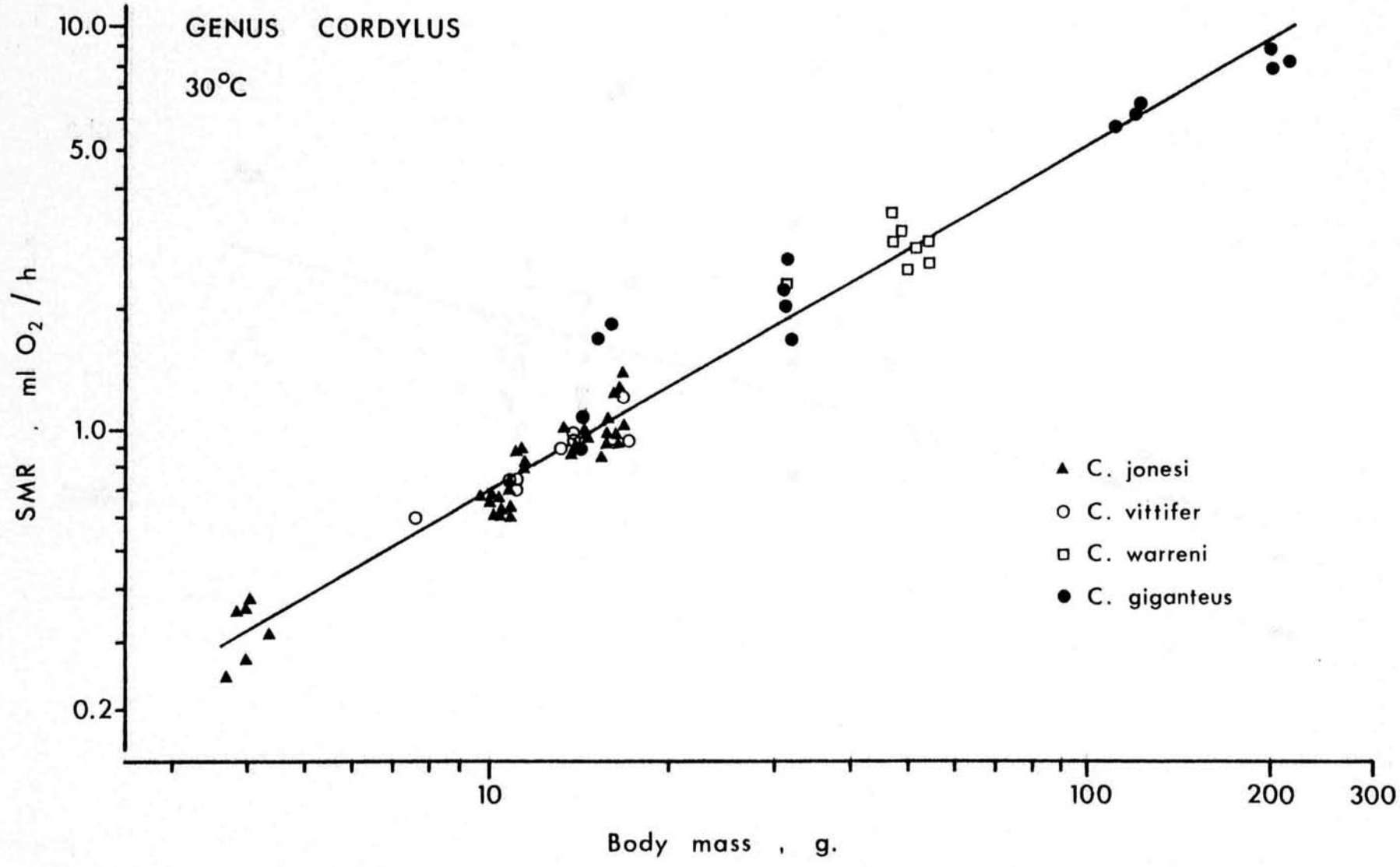

GENUS CORDYLUS
30°C
10.0
5.0
1.0
0.2
SMR . ml O_2 / h
10
100
200
300
Body mass , g.
C. jonesi
C. vittifer
C. warreni
C. giganteus

Fig. 2.17

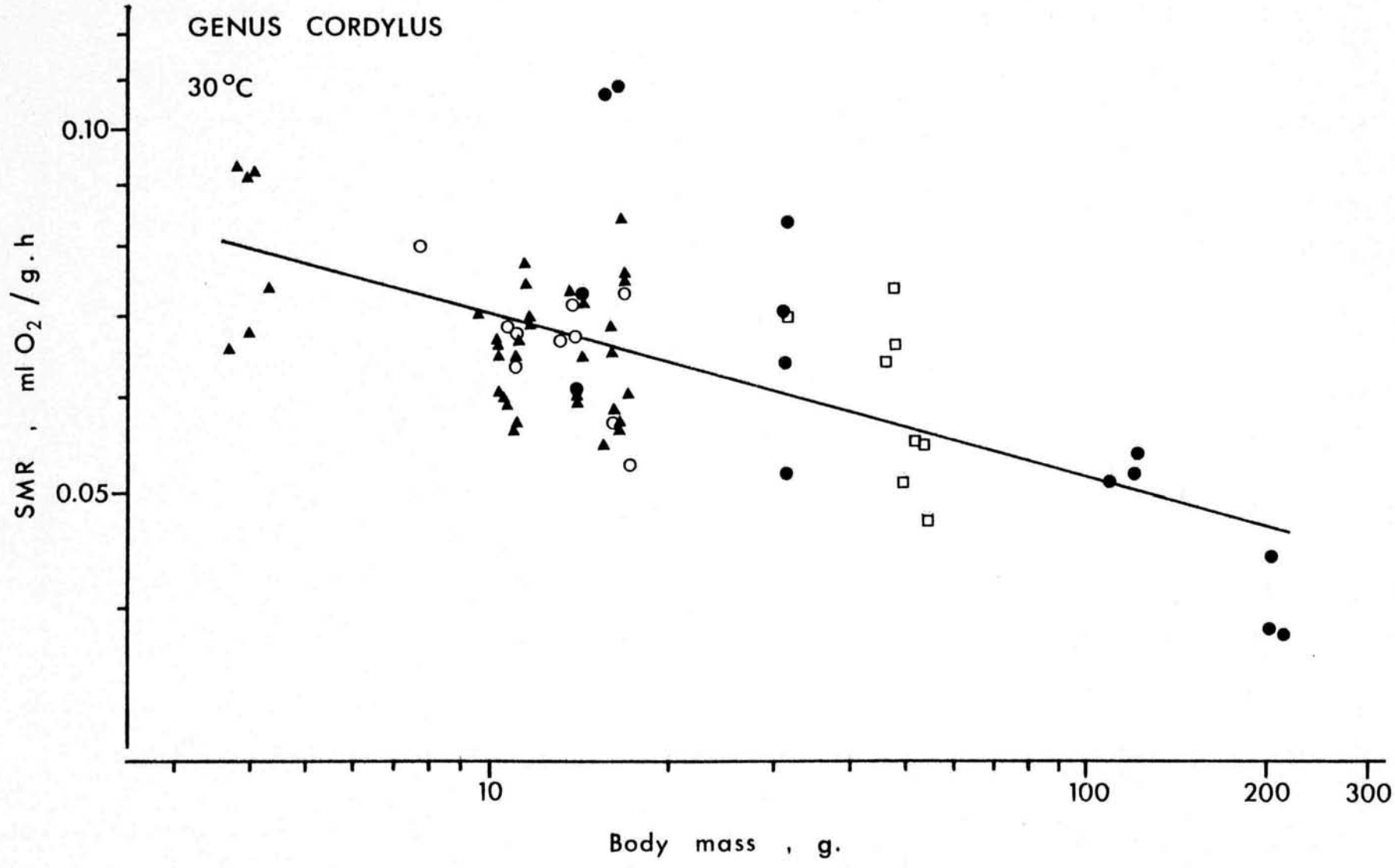

GENUS CORDYLUS
30 °C
0.10
0.05
SMR , ml O_2 / g . h
10
100
200
300
Body mass , g.

Figure 2.18 Relationships of (a) total and (b) mass specific standard metabolic rate to body mass for lizards of the genus *Varanus* at 30°C.

Fig. 2.18

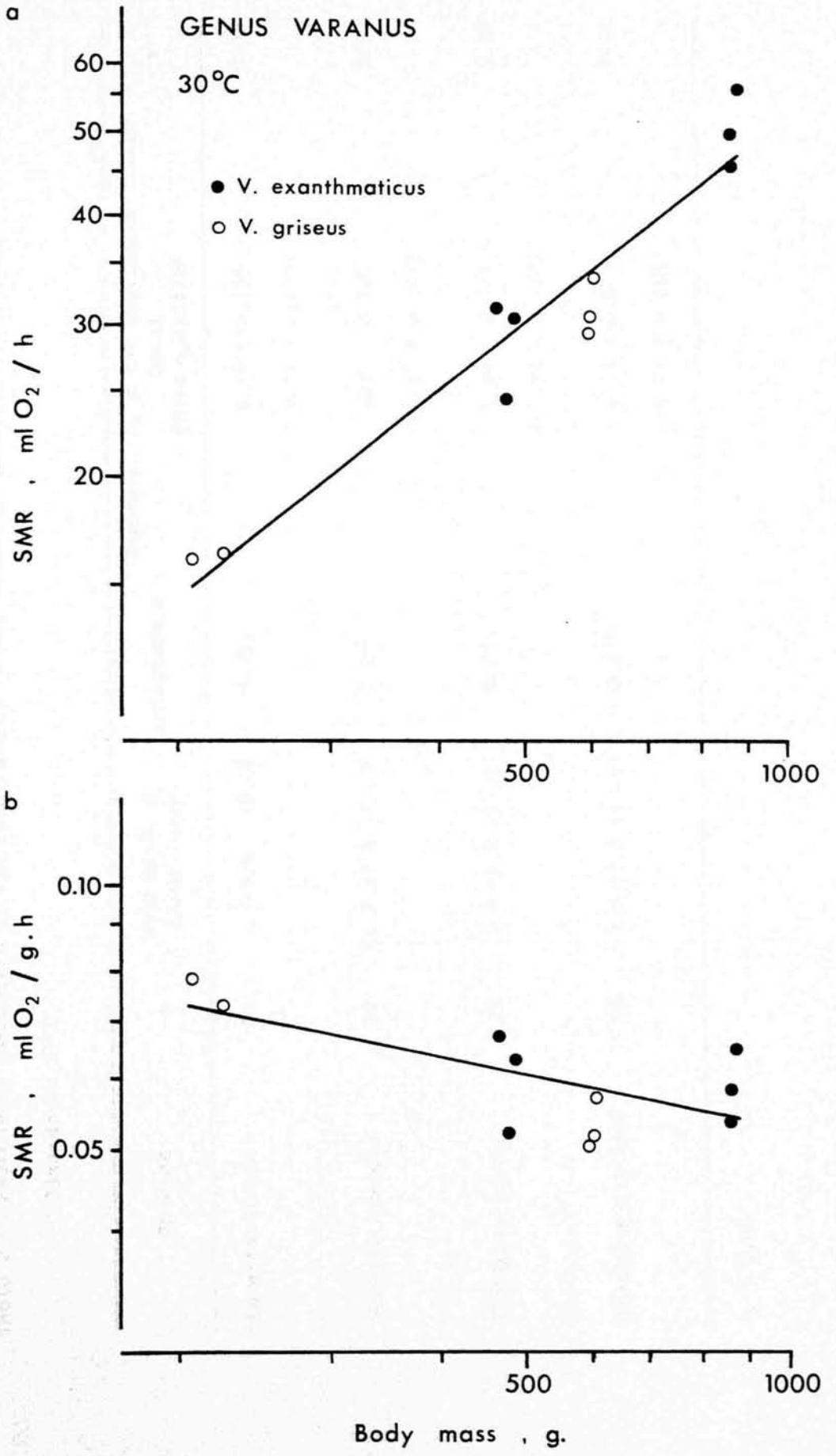

a
GENUS VARANUS
30°C
● V. exanthmaticus
○ V. griseus
60
50
40
30
20
SMR , ml O2 / h
500
1000
b
0.10
0.05
SMR , ml O2 / g.h
500
1000
Body mass , g.

Table 2.5 Regression parameters of the relationship between standard metabolic rate (SMR) and body mass for lizards at 37°C

Species	n	Body mass, g range (mean)	Intercept, a	Exponent, b, ± 95% confidence limits Total (Mass specific)	r
Lacerta sicula	22	3.4-9.6 (6.8)	0.360	0.79 ± 0.13* (-0.21 ± 0.13*)	0.95
Lacerta viridis	30	11.8-37.2 (23.3)	0.290	0.85 ± 0.10* (-0.15 ± 0.10*)	0.95
Cordylus jonesi	26	3.8-16.8 (11.1)	0.175	0.84 ± 0.11* (-0.16 ± 0.11*)	0.96
Cordylus vittifer	13	7.9-17.3 (13.0)	0.275	0.72 ± 0.20* (-0.28 ± 0.20*)	0.92

*$p < 0.05$

Table 2.5 continued

Species	n	Body mass, g range (mean)	Intercept, a	Exponent, b, ± 95% confidence limits Total (Mass specific)	r
Scincus scincus	17	9.7-28.1 (18.9)	0.344	0.77 ± 0.18* (-0.23 ± 0.18*)	0.92
Chalcides ocellatus	28	8.7-34.0 (20.4)	0.297	0.75 ± 0.15* (-0.25 ± 0.15*)	0.89
Tarentola mauritanica	18	7.6-34.7 (22.8)	0.166	0.87 ± 0.19* (-0.13 ± 0.19)	0.93
Agama stellio	10	27.3-55.9 (39.5)	0.410	0.80 ± 0.20* (-0.20 ± 0.20)	0.96

*$p < 0.05$

Figures 2.19-2.26 Relationships of (a) total and (b) mass specific standard metabolic rate to body mass for lizards at 37°C. Heavy lines were fitted by linear regression analysis. The outer pair of lines represent the 95% confidence limits for predicted values of standard metabolic rate.

Figure 2.19 *Lacerta sicula*

Figure 2.20 *Lacerta viridis*

Figure 2.21 *Cordylus jonesi*

Figure 2.22 *Cordylus vittifer*

Figure 2.23 *Scincus scincus*

Figure 2.24 *Chalcides ocellatus*

Figure 2.25 *Agama stellio*

Figure 2.26 *Tarentola mauritanica*

Fig. 2.19

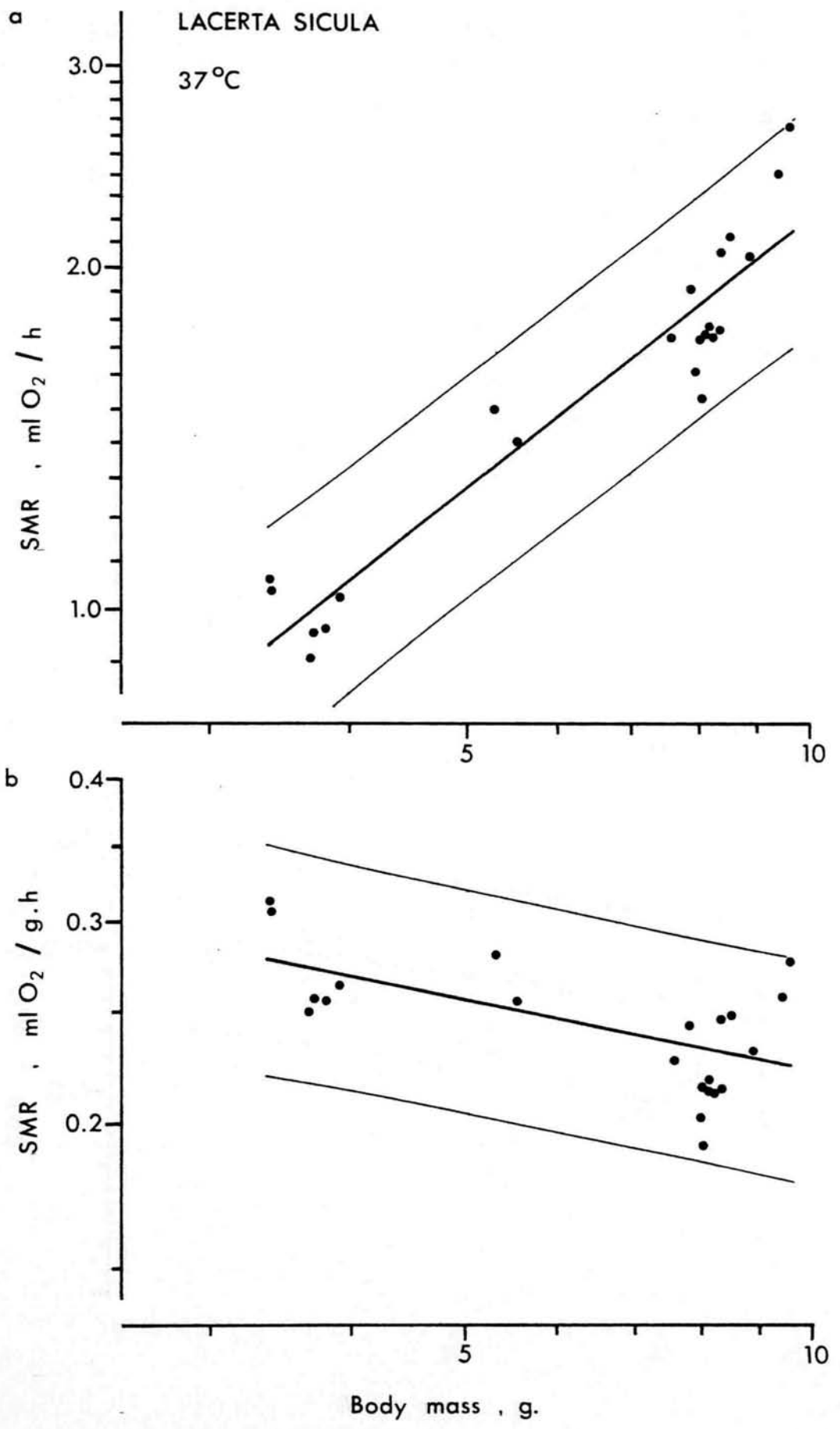

a
LACERTA SICULA
37°C
3.0
2.0
1.0
SMR , ml O_2 / h
5
10
b
0.4
0.3
0.2
SMR , ml O_2 / g.h
5
10
Body mass , g.

Fig. 2.20

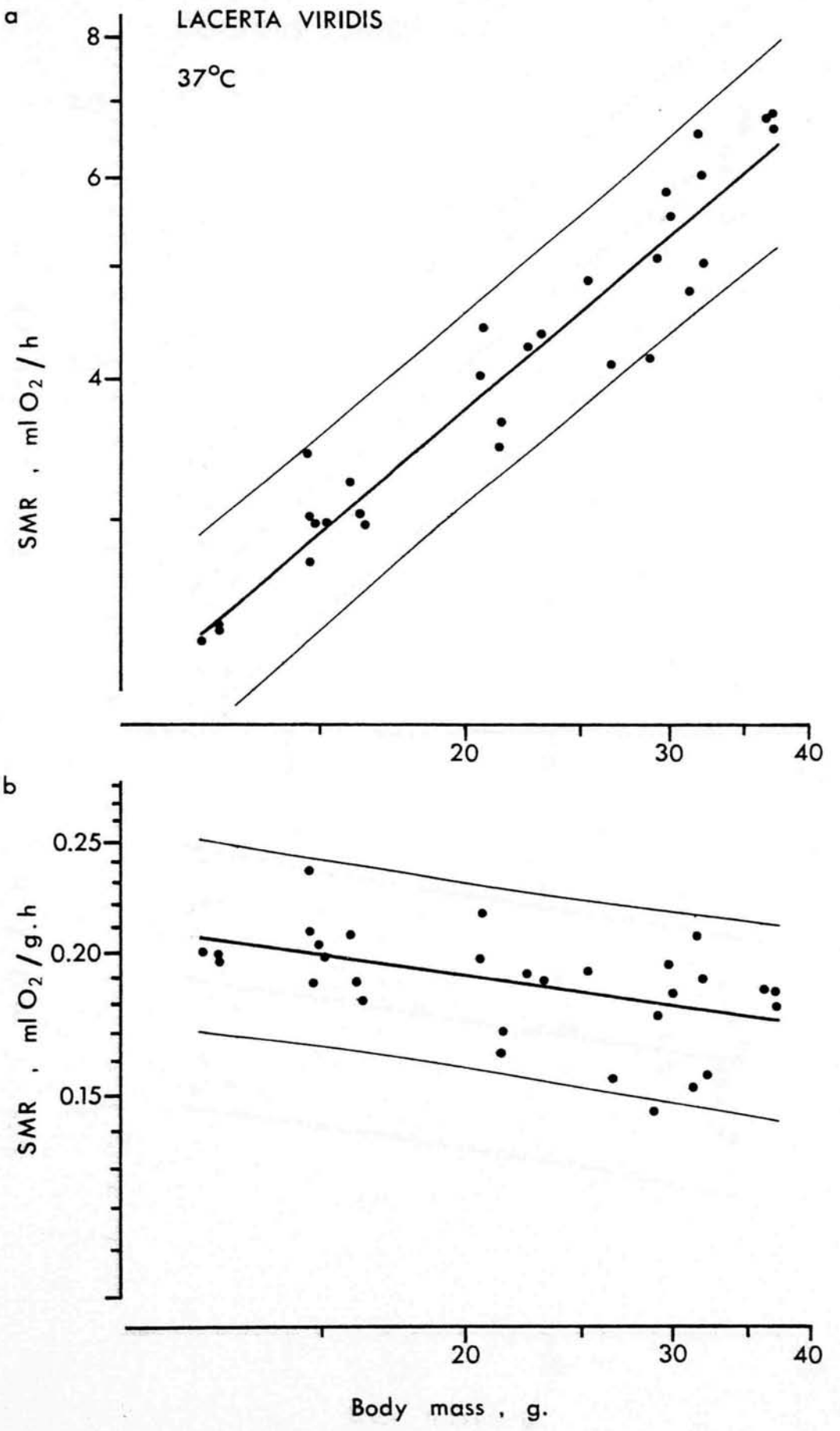

a
LACERTA VIRIDIS
37°C
8
6
4
SMR , ml O2 / h
20
30
40
b
0.25
0.20
0.15
SMR , ml O2 / g.h
20
30
40
Body mass , g.

Fig. 2.21

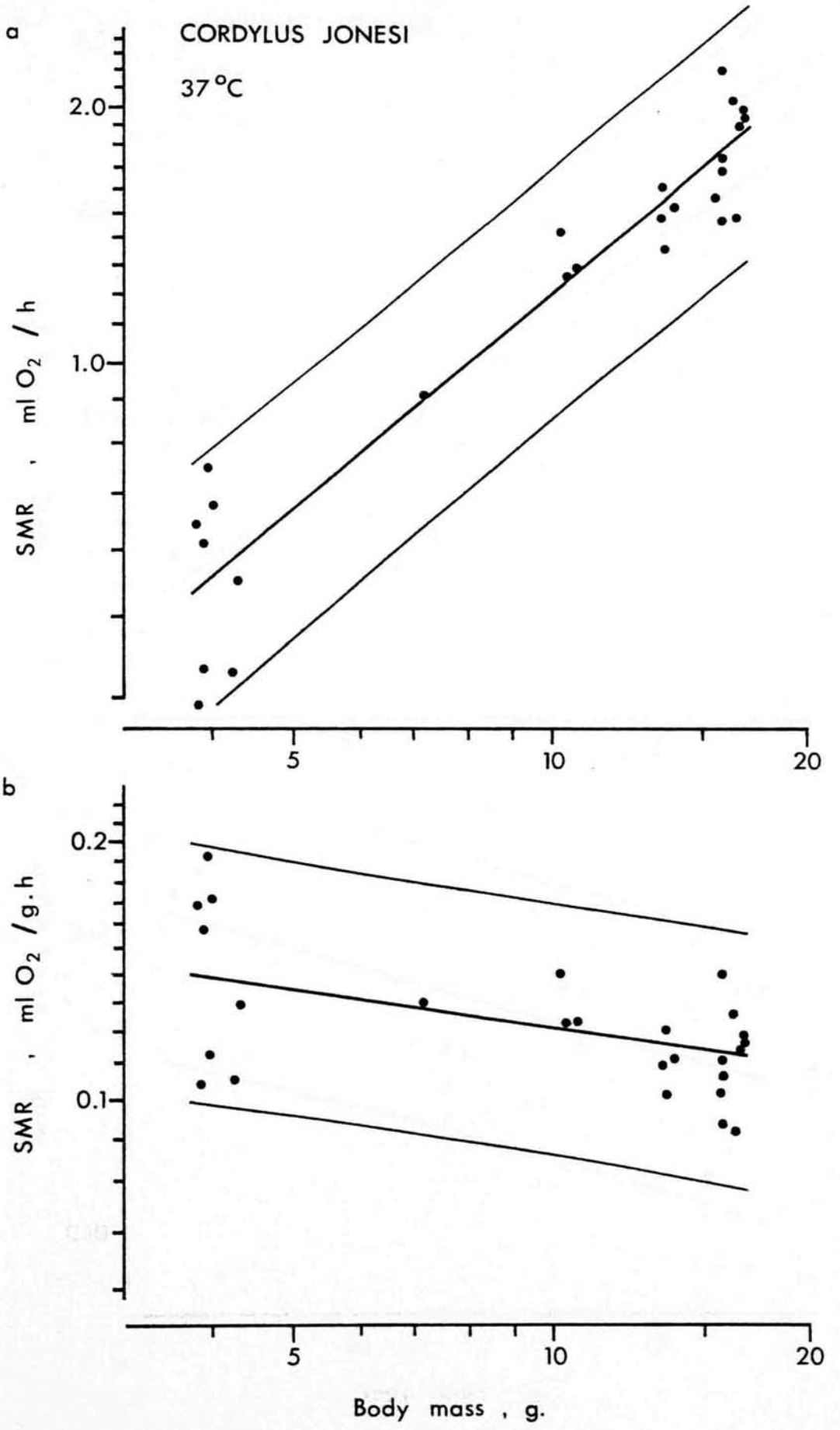

a
CORDYLUS JONESI
37 °C
2.0
1.0
SMR , ml O_2 / h
5
10
20
b
0.2
0.1
SMR , ml O_2 / g.h
5
10
20
Body mass , g.

Fig. 2.22

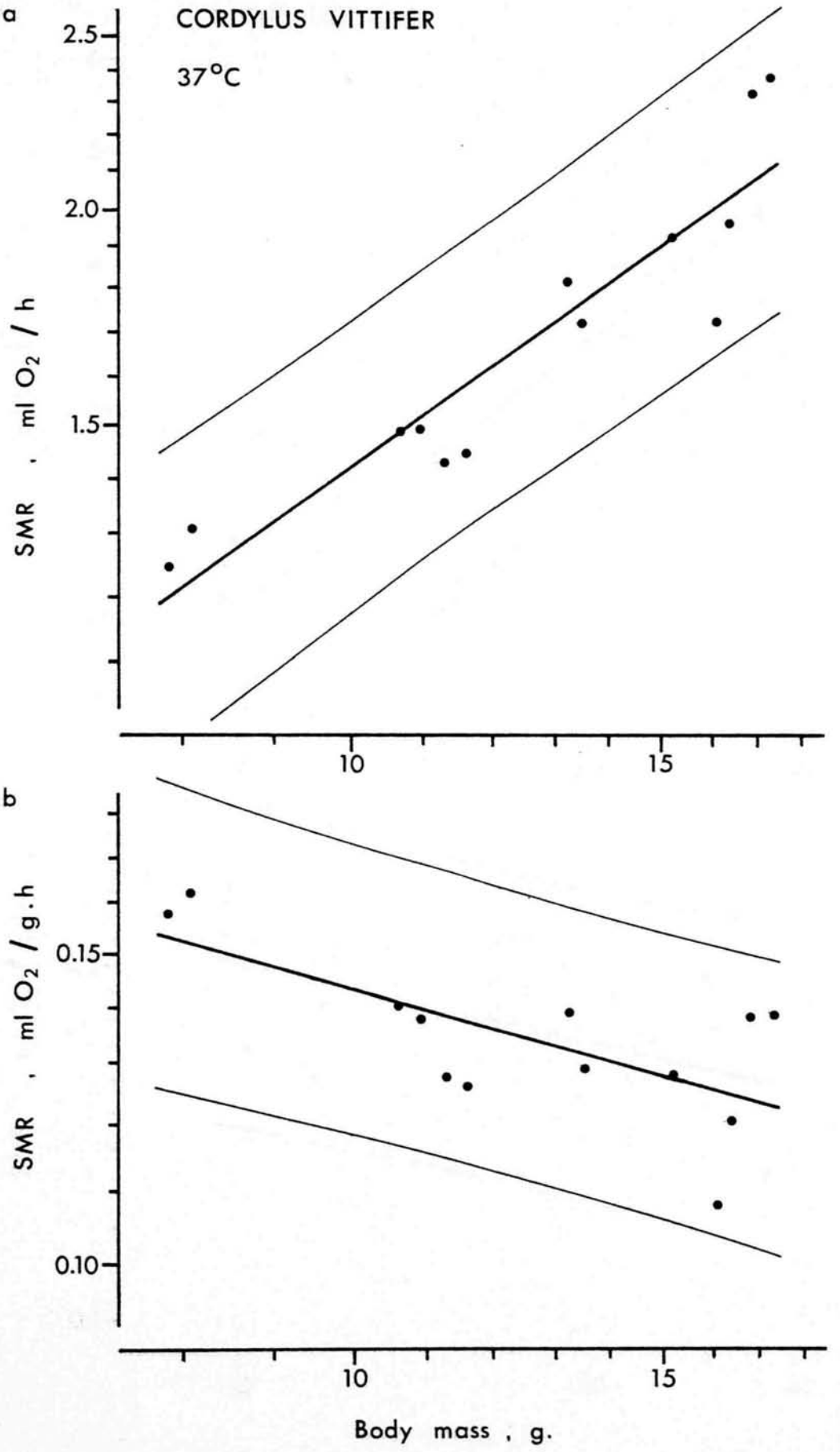

a
CORDYLUS VITTIFER
37°C
2.5
2.0
1.5
SMR , ml O2 / h
10
15
b
0.15
0.10
SMR , ml O2 / g.h
10
15
Body mass , g.

Fig. 2.23

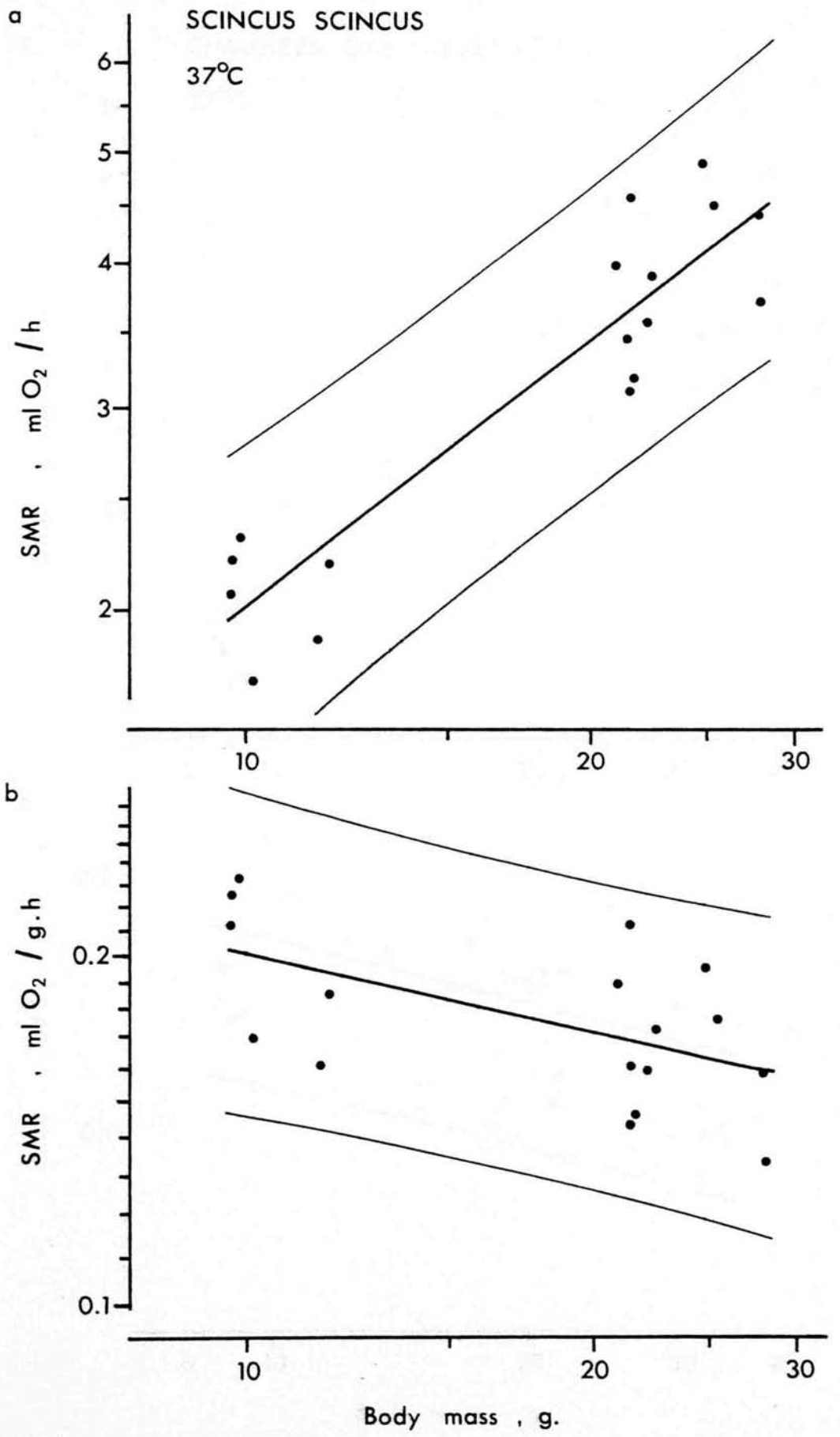

a
SCINCUS SCINCUS
37°C
6
5
4
3
2
SMR , ml O2 / h
10
20
30
b
0.2
0.1
SMR , ml O2 / g.h
10
20
30
Body mass , g.

Fig. 2.24

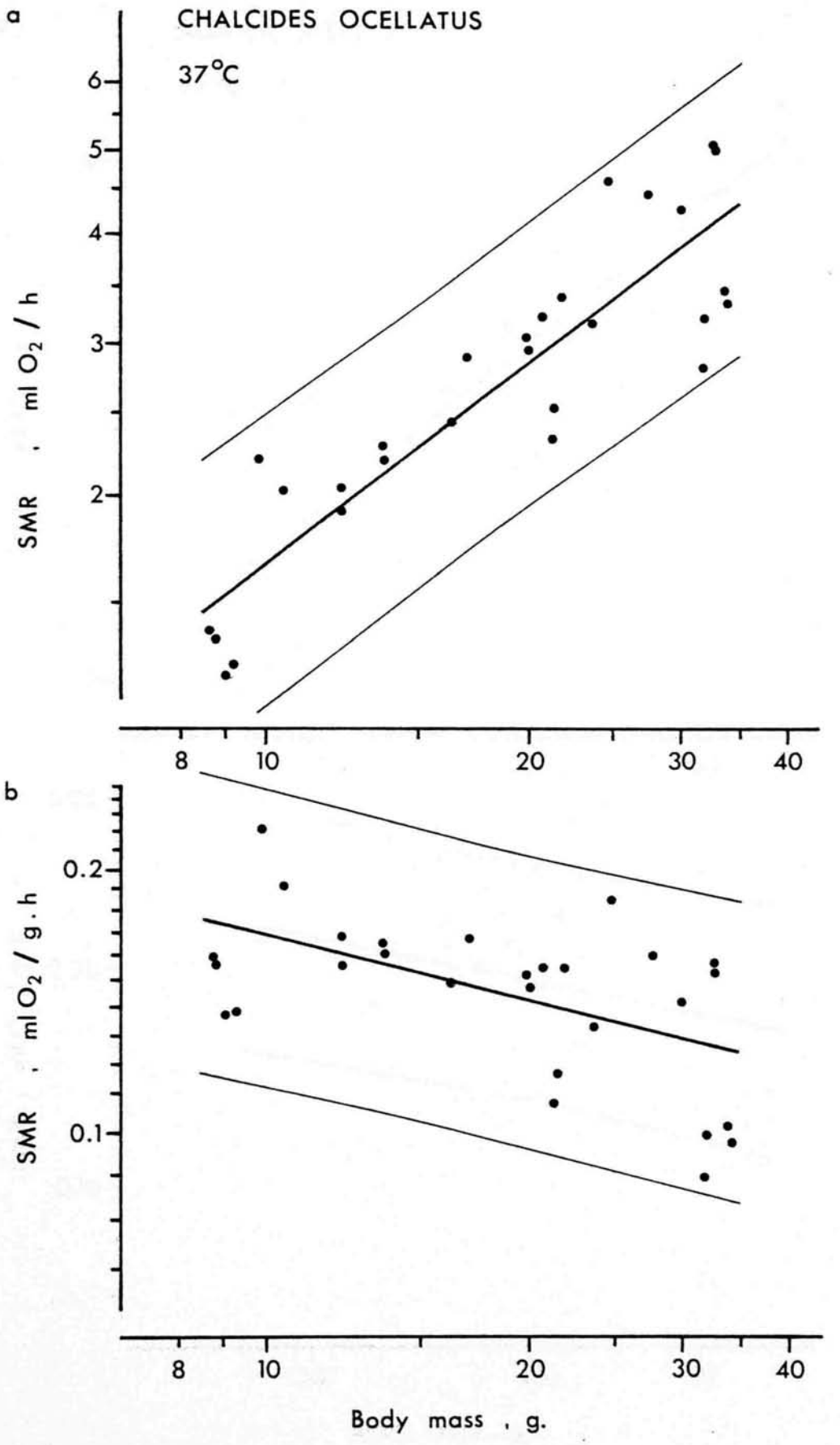

a
CHALCIDES OCELLATUS
37°C
SMR , ml O2 / h
6
5
4
3
2
8
10
20
30
40
b
SMR , ml O2 / g.h
0.2
0.1
8
10
20
30
40
Body mass , g.

Fig. 2.25

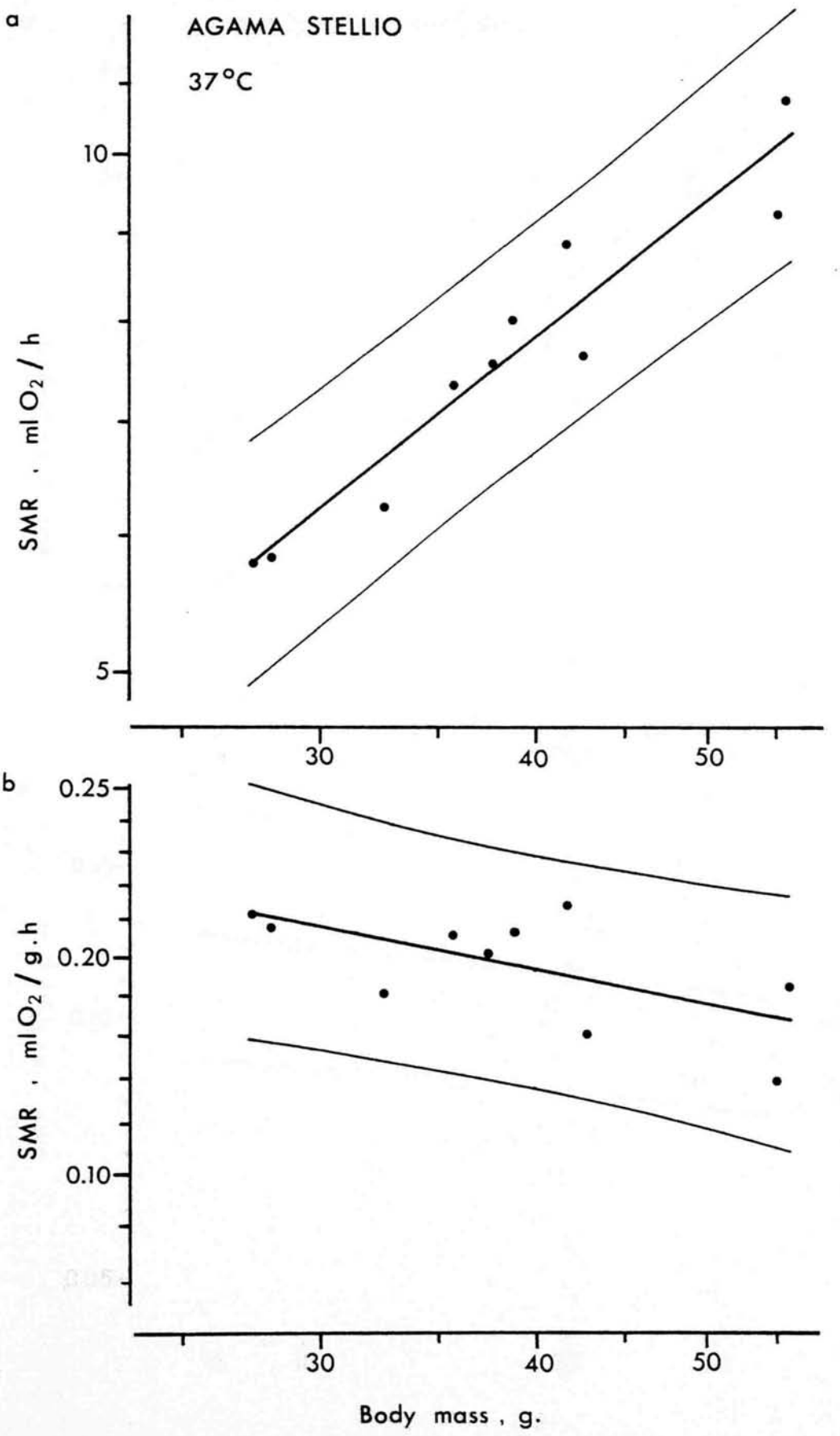

a
AGAMA STELLIO
37°C
10
5
SMR . ml O2 / h
30
40
50
b
0.25
0.20
0.10
SMR . ml O2 / g.h
30
40
50
Body mass , g.

Fig. 2.26

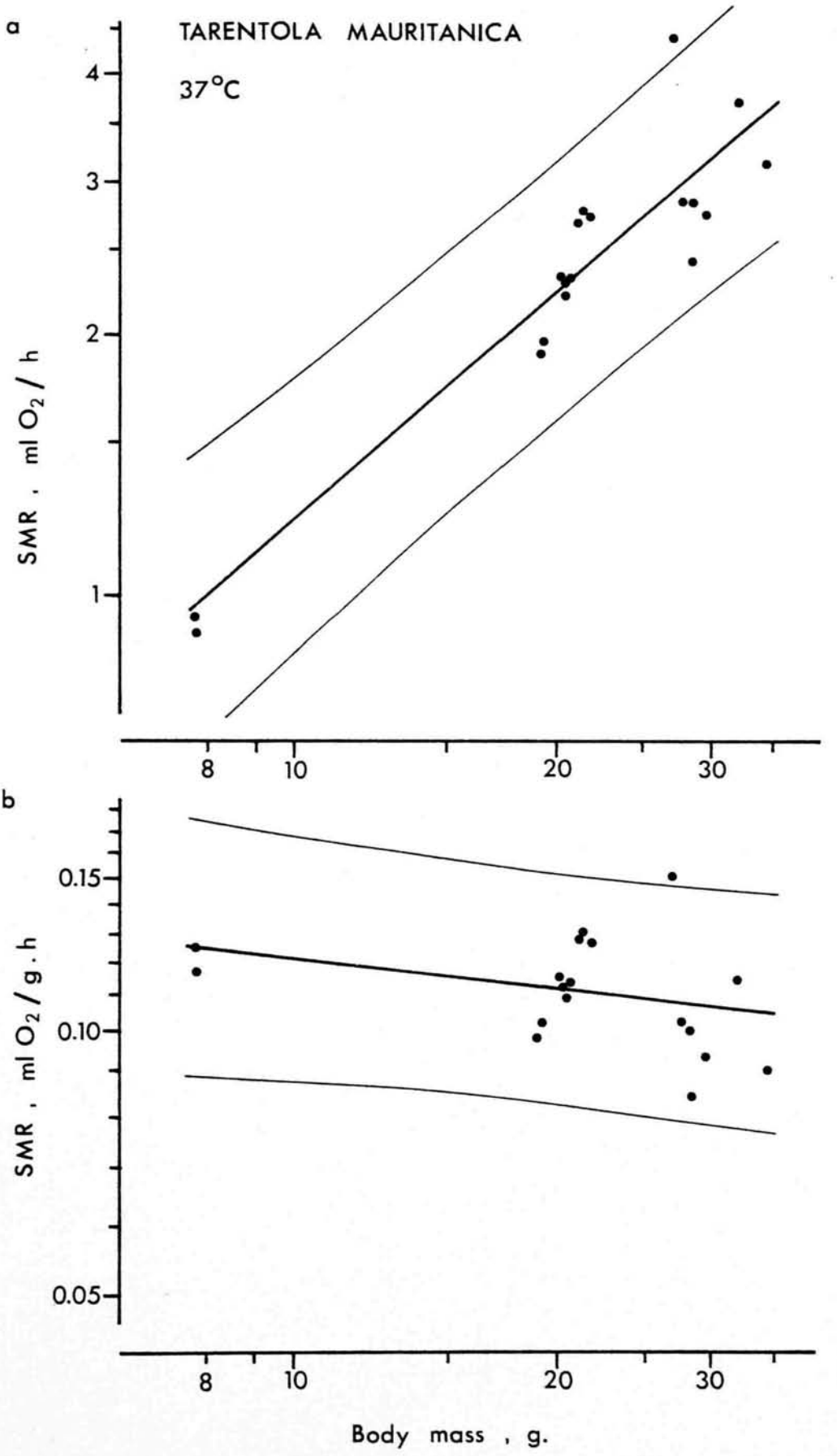

a
TARENTOLA MAURITANICA
37°C
SMR , ml O_2 / h
4
3
2
1
8
10
20
30
b
SMR , ml O_2 / g . h
0.15
0.10
0.05
8
10
20
30
Body mass , g.

Figure 2.27 Relationship of total standard metabolic rate to body mass for lizards of the genus *Lacerta* at 37°C.

Figure 2.28 Relationship of mass specific standard metabolic rate to body mass for lizards of the genus *Lacerta* at 37°C. For key see Fig. 2.27.

Fig. 2.27

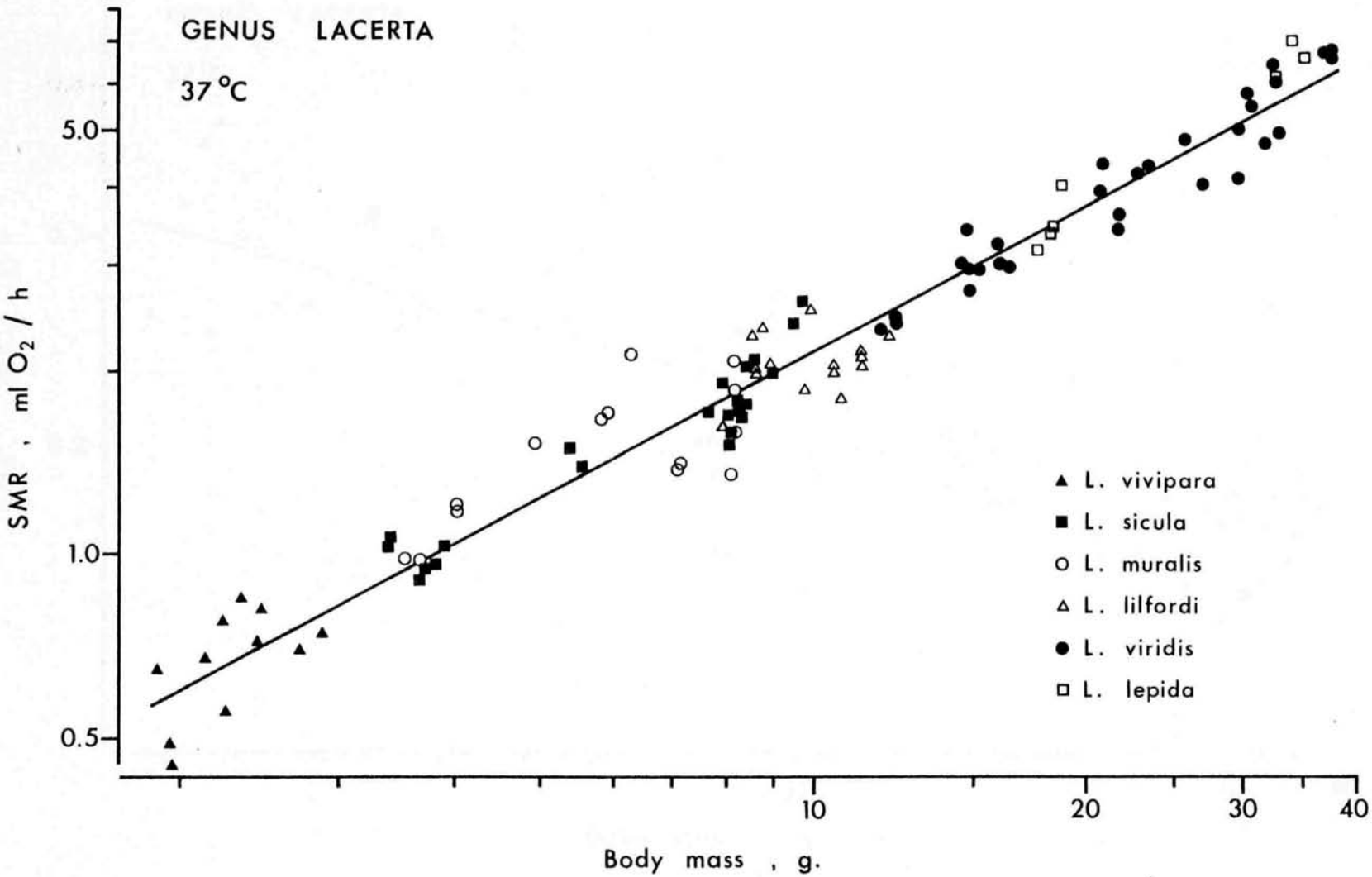
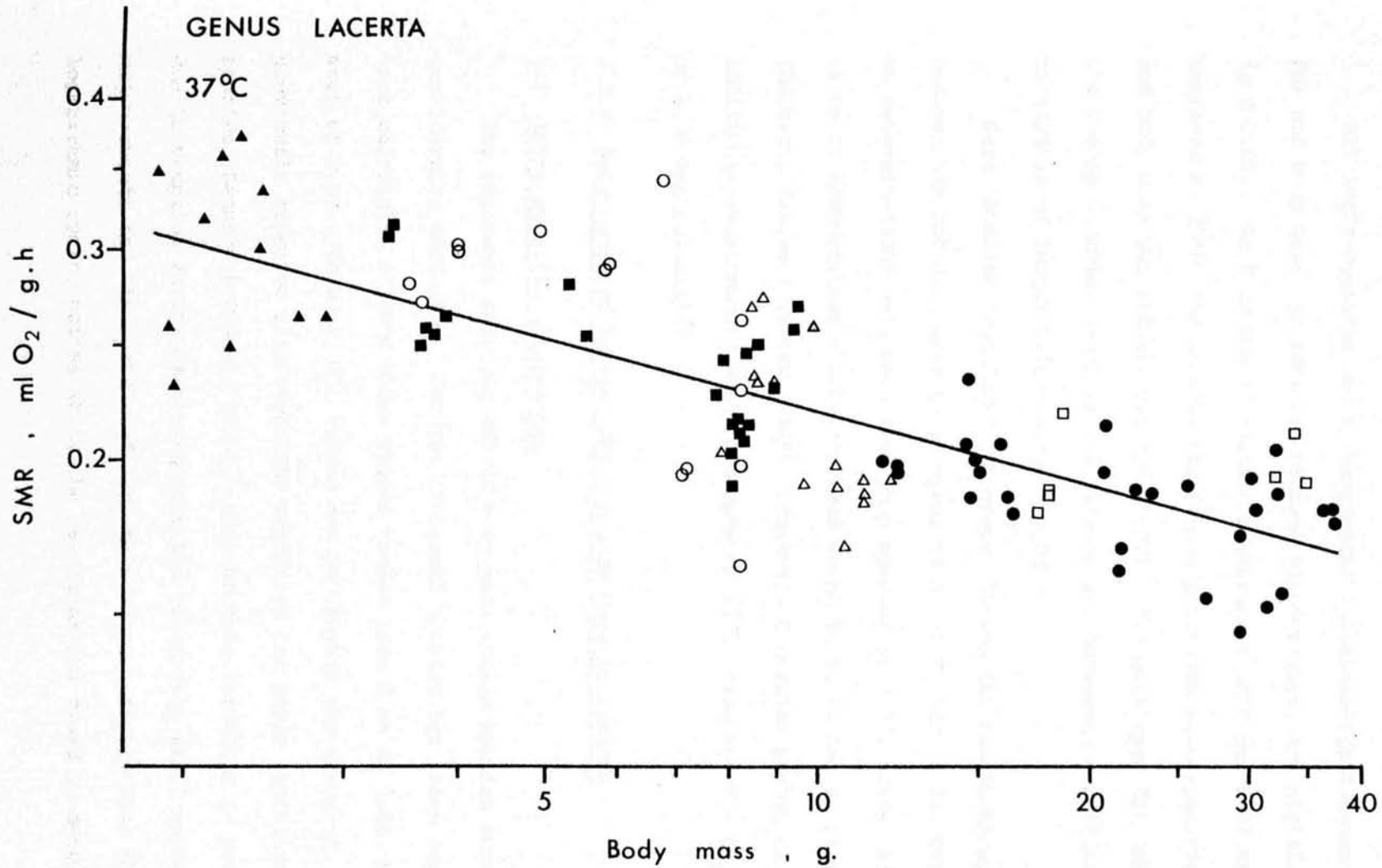

GENUS LACERTA
37 °C
5.0
1.0
0.5
SMR , ml O_2 / h
10
20
30
40
Body mass , g.
L. vivipara
L. sicula
L. muralis
L. lilfordi
L. viridis
L. lepida

Fig. 2.28



generic exponent to be produced for the genus *Lacerta* (Figs. 2.27 & 2.28, Table 2.4).

All intra-specific and intra-generic relationships between total SMR and body mass, at both measurement temperatures, are significant ($p < 0.05$). In 6 of the 11 species measured at 30°C and 6 of the 8 examined at 37°C, the inverse relationship between mass specific SMR and body mass was significant ($p < 0.05$). The mass specific SMRs of the genera *Lacerta*, *Cordylus* and *Varanus* all decreased significantly in animals of larger body size ($p < 0.05$).

Data obtained from *Caiman sclerops* allowed the relationship between SMR and body mass to be examined at 30°C (Fig. 2.29, Table 2.6). No determinations were made from this species at 37°C, since this is close to temperatures which have been found to be lethal to crocodilians (Colbert, Cowles & Bogert, 1946). However, a smaller number of additional measurements were also made at 25°C, from which a Q_{10} value of 2.46 was calculated.

2.3.2 Relationships between SMR and body mass in lizards

(a) Intra-specific allometries

The exponents relating SMR to body mass within species showed considerable variation. For the 11 lizard species for which exponents were calculated at 30°C these values varied from 0.68 to 0.85, with a mean of 0.80. However, all values are well within the range of previously reported intra-specific exponents for other reptilian species (Bennett & Dawson, 1976). Much of this variation is probably due to sampling errors resulting from the relatively small numbers of measurements and the restricted body mass range, usually less than one logarithmic cycle, across which the relationships could be determined,

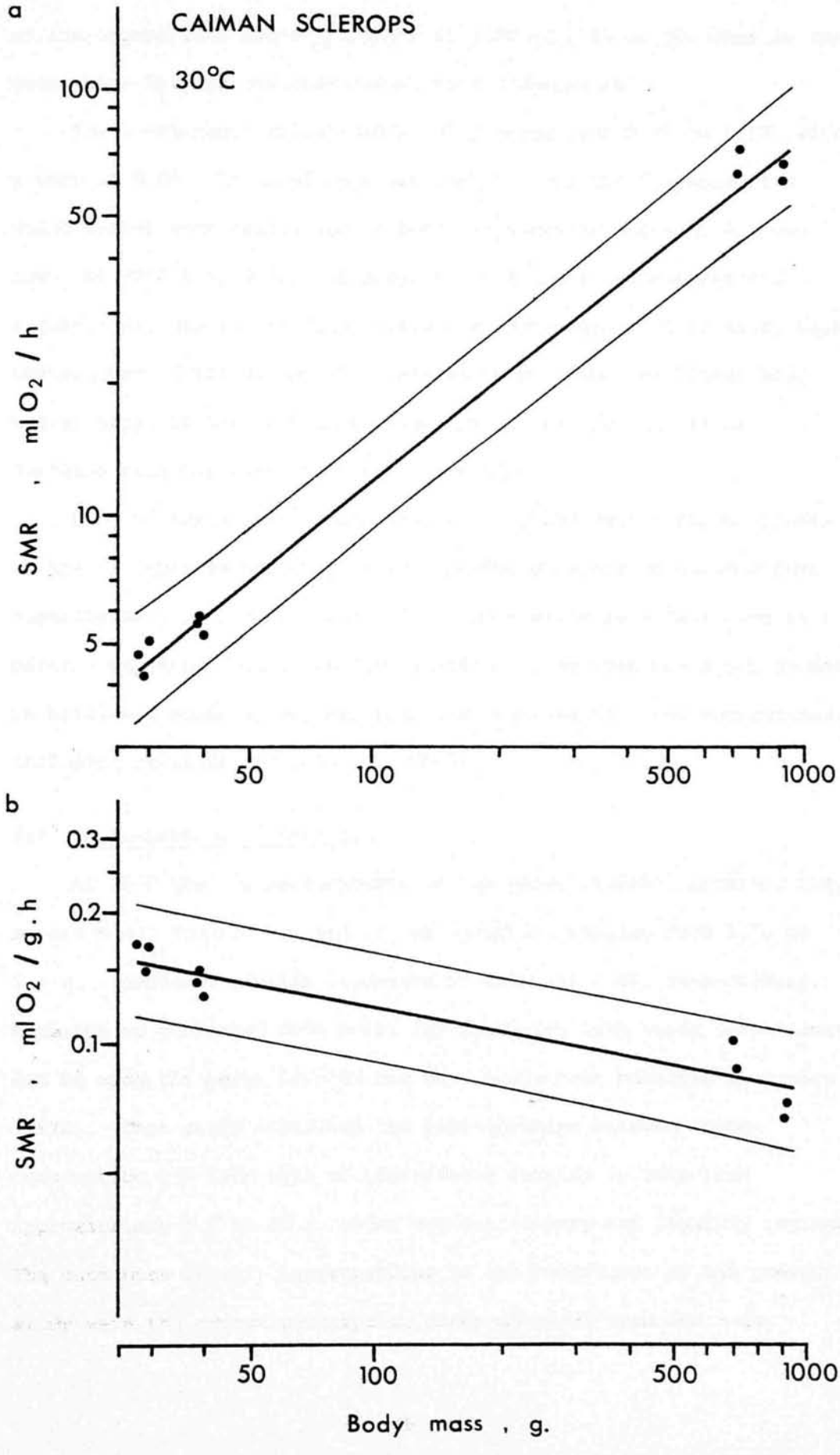
Table 2.6 Regression parameters of the relationship between standard metabolic rate (SMR) and body mass for the crocodilian *Caiman sclerops* at 30° C.

Species	n	Body mass, g range (mean)	Intercept, a	Exponent, b, ± 95% confidence limits Total (Mass specific)	r
Caiman sclerops	10	28.1-930 (350)	0.308	0.80 ± 0.06* (-0.20 ± 0.06*)	0.99

*p < 0.05

Figure 2.29 Relationships of (a) total and (b) mass specific standard metabolic rate to body mass for *Caiman sclerops* at 30°C.

Fig. 2.29


a
CAIMAN SCLEROPS
30°C
100
50
10
5
SMR , ml O2 / h
50
100
500
1000
b
0.3
0.2
0.1
SMR , ml O2 / g . h
50
100
500
1000
Body mass , g.

rather than real metabolic differences between species. The exponent of the crocodilian *Caiman sclerops* at 30°C of 0.80 is the same as the mean value for lizards measured at this temperature.

The 8 exponents calculated at 37°C range from 0.72 to 0.87, with a mean of 0.80. It is of interest that in 7 of the 8 species for which values were calculated at both temperatures the exponent was lower at 37°C than 30°C. Although none of these differences are significant, due to the wide confidence limits attached to each, this convergence of the 30 and 37°C regression equations at higher body masses suggests that within species the Q_{10} of individuals may decrease slightly with increasing body size.

None of the 8 species measured at 37°C and only *Cordylus jonesi* of the 12 reptiles examined at 30°C produced exponents which differ significantly ($p > 0.05$) from 0.75. This value is widely used as a general exponent describing the relationship between BMR and body mass in birds and mammals, and has also been applied to lower vertebrates, including reptiles (Hemmingsen, 1960).

(b) Intra-generic allometries

At 30°C the 109 measurements of the genus *Lacerta*, covering body masses from 1.85 to 37.7 g, and 60 of *Cordylus*, ranging from 3.70 to 214 g, produced similar exponents of 0.85 and 0.86, respectively. Although no published data exist for cordylids with which comparisons can be made, the genus *Lacerta* has previously been examined by Craggs (1978). This study described the relationships between oxygen consumption and body mass of individuals ranging in size from approximately 0.2 to 34 g, under various dietary and lighting regimes. The data most closely corresponding to the conditions of the present study were the oxygen consumption rates obtained from the 3-day

starved animals in a darkened chamber, which gave an exponent of 0.77. The difference between this value and the higher exponent of 0.85 reported here could be a consequence of experimental procedures used in the previous study. The reason for this is that although the *Lacerta viridis* and *L. sicula* used by Craggs (1978) were acclimated to 30°C, the smaller *L. vivipara* were maintained at only 20°C and would therefore have been relatively cold acclimated with respect to the other two species. Any metabolic compensation (see Chapter 5) would have therefore selectively elevated the oxygen consumption of all the individuals of lowest body mass, resulting in a lower exponent than if all the reptiles had been acclimated under standard conditions. Less confidence can be attached to the lower exponent of 0.79 produced for *Varanus* at 30°C than the other two genera, since this was calculated from only 11 measurements of two species. However, this value does not differ significantly ($p > 0.05$) from those of *Lacerta* or *Cordylus*, and is comparable to the 0.82 obtained by Bartholemew & Tucker (1964) from work on 4 species of Australian varanids.

The only intrageneric exponent produced at 37°C was 0.80 for *Lacerta*. This value is significantly ($p < 0.05$) lower than that calculated for the genus at 30°C, which is similar to the trend in the intra-specific exponents already described. This suggests that within genera Q_{10} values may also be less in species of greater body mass.

From comparisons of the small amount of data available on the metabolic rates of immature reptiles with their composite regression equations, Bennett & Dawson (1976) concluded that no well defined metabolic increment associated with the juvenal condition could be demonstrated. In the present study the intra-generic exponents of both *Lacerta* and *Cordylus* were higher than those of their respective

member species, although the differences are not significant ($p > 0.05$) because of the wide confidence limits of the intraspecific values. Within a spcies the smaller individuals are generally the younger animals, and therefore these results indicate that juveniles have a higher SMR than similar sized adults of other species in the same genus. Since the methodology used in the present study enabled resting metabolism to be specifically determined these elevations in the oxygen consumption of younger animals cannot be attributed to higher levels of activity during the measurement period.

In addition to being higher than those of their member species, the exponents of *Cordylus* at 30°C ($p < 0.01$) and *Lacerta* at both 30°C ($p < 0.001$) and 37°C ($p < 0.01$) are significantly closer to unity than is a value of 0.75 (Hemmingsen, 1960).

(c) General exponents for lizards

Heusner (1982) demonstrated that it is not strictly accurate to mathematically describe the relationship between metabolic rate and body mass in larger taxonomic groupings by a single regression equation if its exponent differs from that of the individual member species. However, in practice, the production of a general exponent is extremely useful, since it allows approximate comparisons of metabolism to be made between species of differing body mass.

The first attempt to produce an exponent for lizards by Dawson & Bartholomew (1956), using data from 6 species at 30°C, produced a value of 0.54. This was subsequently revised by Bartholomew & Tucker (1964) to 0.62, after the inclusion of data from an additional 13 species. Templeton (1970) calculated an exponent of 0.65 from measurements of 15 species at the higher temperature of 37°C. These values appear rather low, being considerably less than the exponent of

0.75 associated with higher vertebrates (Kleiber, 1961; Lasiewski & Dawson, 1967). However, the data used to calculate these exponents included few measurements of lizards weighing less than 20 g, and subsequent work on the smaller species involved indicates that the earlier determinations of oxygen consumption used (Gelineo & Gelineo, 1955, Dawson & Bartholomew, 1956) were abnormally high. Consequently, when these data were combined in regression analysis with measurements of larger species they caused an underestimate of the true exponent.

From work on 15 species of lizards at 35°C Vance (1959) produced a composite exponent of 0.87, and Bennett & Dawson (1976) in their review of reptilian metabolism calculated values of 0.80, 0.83 and 0.82 for measurements of lizard metabolic rates at 20, 30 and 37°C, respectively. Although, as already discussed, there are reservations with the latter set which combined data from many diverse sources, both these studies produced values close to the intra-generic exponents reported here.

The present study demonstrates that neither the lizards or the reptiles as a whole can be considered as metabolically homogeneous groups, and it would therefore be inappropriate to produce a general exponent simply by regressing all the data together. Also, the general exponent cannot be calculated from intra-specific values because, as described above, these are lower than those of larger taxonomic groupings, a situation which also exists among mammals (Chapter 3.3.2; Heusner, 1982). The exponent appears to be closer to unity, and therefore proportionality with body mass, than the 0.75 of birds and mammals, which has also been previously applied to reptiles (Hemmingsen, 1960). It is proposed that a general exponent of 0.85 is adopted for lizards. This is intermediate to the values previously

produced by Vance (1959) and Bennett & Dawson (1976), and is similar to the intra-generic exponents for *Lacerta* and *Cordylus* at 30°C, of 0.85 and 0.86 respectively, reported here. If this value is too low the metabolic levels of smaller individuals calculated from it will appear artificially low in comparison with animals of greater body mass. Conversely, their metabolic levels will be elevated if the exponent is too high. The error will increase the greater the size difference of the reptiles under comparison. However, it is felt that the proposed exponent of 0.85 should enable accurate comparisons of lizard species up to at least a body mass of 250 g. Although further work is required, the results of the present study indicate that the exponent may be reduced slightly by increased measurement temperatures.

2.3.3 The standard metabolic levels (SMLs) of lizards and crocodilians

Using the general exponent of 0.85 the standard metabolic level (SML) of each species was determined. The results, presented in Table 2.7, are the means of SML estimates calculated from each measurement of total metabolic rate using the equation:

$$SML = \frac{SMR\ (ml\ O_2/h)}{Mass\ (g)^{0.85}}$$

For the 8 species of reptiles from which determinations were made at both 30 and 37°C Q_{10} values were calculated from the equation:

$$Q_{10} = \frac{SML\ at\ 37°C}{SML\ at\ 30°C}^{\frac{10}{37-30}}$$

These calculations of Q_{10} values assume that between the two temperatures at which measurements were made oxygen consumption

Table 2.7 Standard metabolic levels (SMLs) of lizards and crocodilians at 30 and 37°C calculated using a general exponent of 0.85

Species	SML, mean (± SE, n)		
	30°C	37°C	Q_{10}
Sauria			
Lacerta sicula	0.176 (± 0.005, 20)	0.322 (± 0.007, 22)	2.37
Lacerta muralis	0.168 (± 0.012, 12)	0.337 (± 0.017, 14)	2.70
Lacerta lilfordi	0.166 (± 0.004, 28)	0.302 (± 0.011, 15)	2.35
Lacerta vivipara	0.174 (± 0.007, 14)	0.337 (± 0.016, 11)	2.57
Lacerta viridis	0.174 (± 0.005, 29)	0.298 (± 0.005, 30)	2.12
Lacerta lepida	0.192 (± 0.007, 6)	0.318 (± 0.011, 7)	2.06
Cordylus jonesi	0.096 (± 0.002, 36)	0.171 (± 0.005, 26)	2.28
Cordylus vittifer	0.099 (± 0.003, 9)	0.196 (± 0.005, 13)	2.65
Cordylus warreni	0.108 (± 0.006, 8)		
Cordylus giganteus	0.110 (± 0.007, 15)		
Scincus scincus	0.147 (± 0.006, 17)	0.276 (± 0.009, 17)	2.46
Chalcides chalcides	0.214 (± 0.013, 6)	0.333 (± 0.017, 6)	1.88
Chalcides ocellatus	0.126 (± 0.005, 22)	0.228 (± 0.008, 28)	2.33
Tarentola mauritanica	0.097 (± 0.003, 12)	0.178 (± 0.007, 18)	2.38
Agama stellio	0.185 (± 0.007, 10)	0.341 (± 0.007, 10)	2.40
Chamaeleo chamaeleon	0.230 (± 0.017, 8)		
Anguis fragilis	0.215 (± 0.008, 10)		

Table 2.7 continued

Species	SML, mean (± SE, n)		
	30°C	37°C	Q_{10}
Varanus griseus	0.150 (± 0.007, 5)	2.88 (± 0.012, 3)	2.54
Varanus exanthmaticus	0.157 (± 0.009, 6)		
Crocodilia			
Caiman sclerops	0.245 (± 0.009, 10)	0.156* (± 0.008, 5)	2.46*

*relate to measurements at 25°C

is exponentially related to body temperature and there are no metabolic plateaus, similar to those reported by Aleksiuk (1971), Tromp & Avery (1977) and Brown & Loveridge (1981). The resulting Q_{10} values varied from 1.9 to 2.9, and are therefore within the range previously reported for reptiles (Dawson, 1975). The mean lizard Q_{10} of 2.36 is similar to the composite value of 2.12 calculated across the temperature range of 30 to 37°C by Bennett & Dawson (1976). The Q_{10} for *Caiman sclerops* of 2.46 was calculated across the lower temperature range of 25 to 30°C.

Metabolic levels of lizards at 30°C calculated from data reported in some earlier studies are presented in Table 2.8 and Fig. 2.30. This list is not intended to be an exhaustive review of the literature, but to give an idea of the range of values previously found in different families. When making comparisons between studies it should be remembered that although all data relate to resting metabolism the conditions under which measurements were made are not necessarily the same as those used to determine SMLs in the present study. All estimates of metabolic levels were calculated using an exponent of 0.85. For some studies in which measurements were not actually made at 30°C the metabolic levels are based on interpolations or extrapolations of data obtained in the temperature range of 25 to 35°C. In a few cases it was necessary to estimate metabolic rates at 30°C using the mean Q_{10} value calculated in the present study from lizards of the appropriate family.

Where direct comparisons can be made with data collected under similar conditions, for example lacertids (Craggs, 1978) and small rodents (Chapter 3.3.3), the agreement between the results of this and other studies is extremely good. This gives a high level of

Table 2.8 Standard metabolic levels (SMLs) of lizards at 30°C calculated using a general exponent of 0.85 from data presented in previous studies obtained under conditions approximately comparable to those used in the present study

Species	Body mass, g.	SML	Reference
Lacertidae			
Lacerta sp	10	0.180	Craggs (1978)
Scincidae			
Acontias melagris	7.3	0.106	Withers (1981)
Acontias melagris	7.3	0.101	Brownlie & Loveridge (1983)
Egernia cunninghami	261	0.200	Wilson (1971,1974)
Eumeces fasciatus	7.0	0.321	Maher (1965)
Eumeces obsoletus	30	0.283	Dawson (1960)
Mabuya sp.	10.2	0.176	Withers (1981)
Mabuya capensis	9.2	0.151	Brownlie & Loveridge (1983)
Proscelotes arnoldi	4.6	0.113	Brownlie & Loveridge (1983
Scelotes gronovii	1.1	0.210	Withers (1981)

Table 2.8 (continued)

Species	Body mass, g.	SML	Reference
Scincidae (continued)			
Scincella lateralis	1.0	0.306	Hudson & Bertram (1966)
Tiliqua scincoides	493	0.228	Bartholomew et al (1965)
Typhlosaurus cregoi	5.5	0.097	Brownlie & Loveridge (1983)
Xantusiidae			
Xantusia vigilis	1.1	0.132	Snyder (1971)
Gekkonidae			
Anarbylus switaki	9.5	0.160	Putnam & Murphy (1982)
Coleonyx variegatus	3.6	0.275	Putnam & Murphy (1982)
Cosymbotus platyurus	1.2	0.151	Feder & Feder (1981)
Gonatodes antillensis	1.0	0.159	Bennett & Gorman (1979)
Hemidactylus frenatus	0.7	0.215	Feder & Feder (1981)
Lepidodactylus lugubris	0.7	0.170	Feder & Feder (1981)

Table 2.8 (continued)

Species	Body mass, g.	SML	Reference
Gekkonidae (continued)			
Sphaerodactylus beattyi	0.4	0.224	Snyder (1979)
Sphaerodactylus macrolepsis	0.5	0.222	Snyder (1975)
Agamidae			
Amphibolurus barbatus	373	0.238	Bartholomew & Tucker (1963)
Physignathus lesueurii	504	0.203	Wilson (1971,1974)
Iguanidae			
Anolis carolinensis	4.5	0.238	Maher & Levedahl (1959)
Cnemidophorus tigris	18	0.215	Asplund (1970)
Crotaphytus collaris	30	0.300	Dawson & Templeton (1963)
Dipsosaurus dorsalis	51.3	0.163	Moberly (1963)
Iguana iguana	795	0.221	Moberly (1968)
Phrynosoma mcalli	15.6	0.257	Mayhew (1965)

Table 2.8 (continued)

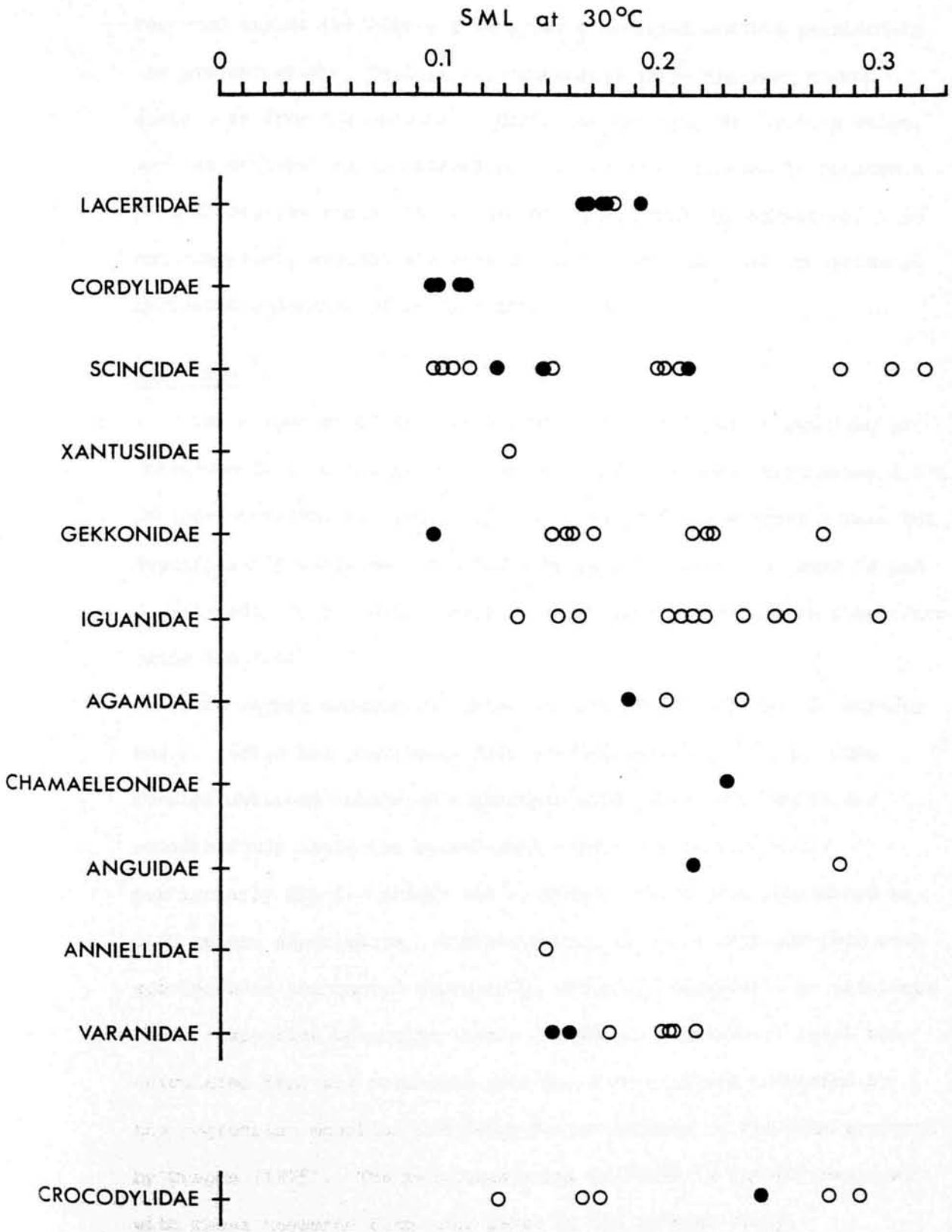
Species	Body mass, g.	SML	Reference
Iguanidae			
Sauromalus hispidus	574	0.135	Bennett (1972a)
Sauromalus obesus	150	0.153	Boyer (1967)
Sceloporus graciosus	5.0	0.210	Mueller (1969)
Uta mearnsi	14	0.253	Murrish & Vance (1968)
Uta stansburiana	3.0	0.204	Roberts (1968)
Anguidae			
Gerrhonotus multicarinatus	29.4	0.282	Dawson & Templeton (1966)
Anniellidae			
Anniella pulchra	4.9	0.147	Fusari (1984)

Table 2.8 (continued)

Species	Body mass, g.	SML	Reference
Varanidae			
Varanus bengalensis	3440	0.176	Earll (1982)
Varanus exanthmaticus	1000	0.204	Wood et al (1978)
Varanus exanthmaticus	1650	0.200	Rome (1982)
Varanus gouldii	674	0.205	Bennett (1972a)
Varanus salvator	505	0.216	Gleeson (1981)

Figure 2.30 Metabolic levels of reptiles at 30 ℃ obtained in the present study (● , see Table 2.7) or calculated from data presented by previous workers (O , see Table 2.8 & 2.9).

Fig. 2.30


SML at 30°C
0
0.1
0.2
0.3
LACERTIDAE
CORDYLIDAE
SCINCIDAE
XANTUSIIDAE
GEKKONIDAE
IGUANIDAE
AGAMIDAE
CHAMAELEONIDAE
ANGUIDAE
ANNIELLIDAE
VARANIDAE
CROCODYLIDAE

confidence in the techniques and procedures used, and consequently in the data obtained from other reptilian species. Some of the previously reported values are higher than those of related species examined in the present study. This is not unexpected since the most common deviations from the condition adopted as defining SML in this study, such as acclimation to temperatures below 30°C, failure to achieve a post-absorptive state and the use of measurement procedures which do not completely exclude activity metabolism will all tend to produce increased estimates of resting metabolism.

Lacertids

The 6 species of this exclusively Old World family examined all possessed SMLs in the range 0.166 to 0.192, the mean value being 0.175. *Lacerta vivipara*, *L. viridis* and *L. lepida* did not possess a mean SML significantly different from the 3 species *L. sicula*, *L. muralis* and *L. lilfordi* ($p > 0.005$), which are sometimes classified in a separate genus *Podarcis*.

The oxygen consumption rates at 30°C of *L. vivipara*, *L. viridis* and *L. sicula* has previously been studied by Craggs (1978). The results obtained should be comparable with those produced by the present study since the measurement conditions were similar, particularly for *L. viridis* and *L. sicula* which were acclimated to 30°C before experiments. Unfortunately, the data obtained from each species were not quoted separately, making it impossible to calculate their respective metabolic levels. However, a metabolic level was calculated from the metabolic rate for a 10 g lizard predicted by the regression equation for 3-day fasted animals in the dark produced by Craggs (1978). The resulting value of 0.180 is almost identical with those measured from this genus in the present study.

Cordylids

There are no previously reported measurements of this little studied family of African lizards. All species used in this study were from the genus *Cordylus* which, despite considerable differences in size, are morphologically very similar. None of the differences between the SMLs of the 4 species examined, which ranged from 0.096 to 0.110, were significantly different ($p > 0.05$). In addition to being relatively homogeneous the metabolic levels of these cordylids are also very low. The mean SML for this genus is 0.103, only about 60% of that calculated for the genus *Lacerta*. One contributory factor to the low SML of this genus could be their possession of well developed protective dermal armour, which means that the proportion of their total body mass comprised of relatively metabolically inert tissues is greater than for most other lizards.

Scincids

The skinks are a morphologically and ecologically very diverse family of lizards with a worldwide distribution. This variation in body form and habitat is reflected in the wide range of metabolic levels which have been reported for members of this family. The SMLs of the 3 European and North African skinks examined here are similar to values found for South African species (Withers, 1981; Brownlie & Loveridge, 1982), and considerably lower than those found in some earlier studies of North American and Australian forms (Dawson, 1960; Maher, 1965; Bartholomew, Tucker & Lee, 1965; Wilson, 1971, 1974).

Chalcides ocellatus and *C. chalcides* are the only members of a single genus examined in the present study which display large significant differences in SML ($p < 0.001$). However, unlike the lacertids, cordylids and varanids, there are also marked anatomical

differences between these two scincids; *C. chalcides* is long, thin and possesses only small vestigial limbs, unlike its stockier and more typically lizard-like relative *C. ocellatus*. These differences in structure could be associated with changes in the relative proportions of metabolically active tissues, which would contribute to their different SMLs. A similar situation has been found in South African scincids, among which the monodactylus species *Scelotes gronovii* has a higher metabolic level than tetrapodous skinks of the genus *Mabuya* (Withers, 1981). The metabolic level calculated from data on *Scelotes gronovii* is 0.210, a value similar to that of 0.214 reported here for *C. chalcides*. However, it should be noted that the completely limbless form *Acontias melagris* has been found to possess a relatively low metabolic level (Withers, 1981; Brownlie & Loveridge, 1982).

Gekkonids

The majority of the species in this widespread family, including *Tarentola mauritanica* , are predominantly nocturnal. Many, although not all, geckos previously examined have been recognised as possessing lower metabolic levels than most other lizards (Feder & Feder, 1981; Putnam & Murphy, 1982). This was also the case for *T. mauritanica* measured in the present study, which displayed the lowest SML yet reported for a gekkonid.

Agamids

Agama stellio, the only member of this exclusively Old World family examined, possessed a SML only slightly lower than those previously found in the two large Australian species *Amphibolurus barbatus* (Bartholomew & Tucker, 1963) and *Physignathus lesueurii* (Wilson, 1971, 1974). These metabolic levels lie close to the middle

of the range of values reported for iguanids, a related family occupying many similar niches in the New World.

Chamaeleonids

Only a single species of chamaeleon was available for the present study, and no metabolic measurements of these lizards have previously been reported. This lack of data on these lizards may partially be due to the difficulties of maintaining them in captivity for long periods. These slow-moving reptiles unexpectedly displayed the highest SML of all the species examined. However, it is possible that the unusual posture of these lizards could be the reason for their high SML. Most lizards possess a sprawling gait, only raising their bodies above the ground while walking or running. Chamaeleons are the only reptiles which maintain an erect posture for long periods, even while stationary. The high oxygen consumption of these lizards could reflect the additional energetic demands of the skeletal musculature required to hold the body in this position. It has been suggested that muscle tonus associated with posture is a major contributory factor to the high BMLs of mammals and birds, the only other vertebrates with an erect stance (Heath, 1968).

Anguids

The legless snake-like form *Anguis fragilis* possessed a relatively high SML of 0.215. This is the same as that of the morphologically and ecologically similar, but unrelated, scincid *Chalcides chalcides*. The North American anguid *Gerrhonotus multicarinatus*, which has four limbs of slightly reduced proportions, has an even higher metabolic level of 0.282 (Dawson & Templeton, 1966).

Varanids

Early measurements of Australian varanids (Bartholomew & Tucker, 1964) suggested that they possessed unusually high metabolic levels, but subsequent work on one of these species, *Varinus gouldi* (Bennett, 1972a), found oxygen consumption levels comparable to those of other lizards. This agrees with the results of the present study, in which SMLs of *Varanus griseus* and *V. exanthmaticus* are near the middle of the range of values for lizards at 30°C. However, the metabolic levels of these two species are slightly lower than those previously reported for members of this genus. This may be because the techniques adopted by several of these studies (Bennett, 1972a; Rome, 1982; Gleeson, 1981) were primarily designed to measure activity metabolism rather than make accurate determinations of resting metabolic rate. These involved the use of masks to measure oxygen consumption, often over very short measurement periods, from animals which were not necessarily in a post-absorptive state. Two previous studies on *V. exanthmaticus* have produced estimates of metabolic level 25-30% above that reported here, although these were measured under conditions different from those adopted as standard in the present study; Rome (1982) monitored the resting oxygen consumption of non-fasted animals for only 30 minutes using a mask, and the lizards used by Wood *et al* (1978) were maintained in non-darkened chambers and radiantly heated during experiments.

Although the following families have been previously examined by other workers no representatives were included in the present study.

Xantusids

This New World family of small nocturnal lizards are similar in appearance to the gekkonids, with many of which they also share a relatively low metabolic level. Originally it was throught that the xantusids were exceptional in this respect (Snyder, 1971; Bennett & Dawson, 1976), but subsequent measurements of gekkonids and cordylids have shown that reduced oxygen consumption rates are more widespread among lizards.

Iguanids

These predominantly New World lizards have been well represented in earlier studies. The relatively large amount of data produced indicates that, like the scincids, they are a metabolically, as well as morphologically and ecologically, very heterogeneous group.

Anniellids

This North American family is closely related to the anguids. They resemble *Anguis fragilis* in appearance, but are even more highly adapted to a burrowing mode of life. However, unlike *A. fragilis*, *Anniella pulchra* possesses a relatively low metabolic level of 0.147 (Fusari, 1983). Therefore, there does not appear to be a simple correlation between a legless snake-like morphology and either a high or low metabolism.

There are few data on crocodilian metabolism obtained under standard conditions, since the studies on this group have been conducted at various temperatures in the range 18 to 37°C (Huggins, Hoff & Valentinuzzi, 1971) using very diverse measurement techniques and procedures. The estimates of metabolic levels, presented in

Table 2.9 Standard metabolic levels (SMLs) of small crocodilians at 30°C calculated using a general exponent of 0.85 and a Q_{10} value of 2.46 from data presented in previous studies.

Species	Body mass, g.	SML	Reference
Caiman sclerops (summer)	161	0.164	Hernandez & Coulson (1952)
Caiman sclerops (winter)	116	0.172	Hernandez & Coulson (1952)
Caiman sclerops	124	0.291	Bentley & Schmidt-Nielsen (1966)
Caiman sclerops	274	0.277	Huggins, Hoff & Valentinuzzi (1971)
Caiman sclerops	749	0.125	Huggins, Valentinuzzi & Hoff (1971)
Alligator mississippiensis (summer)	87.7	0.172	Hernandez & Coulson (1952)
Alligator mississippiensis (winter)	49.7	0.172	Hernandez & Coulson (1952)

Table 2.9, were calculated from the data presented in earlier studies using a Q_{10} of 2.46 and an exponent of 0.85. Since the general exponent relating SMR to body mass in crocodilians may be different from that of lizards data from very large specimens (Buytendijk, 1910; Benedict, 1932; Grigg, 1978; Brown & Loveridge, 1981) has not been used, and comparisons are confined to individuals weighing less than 1,000 g. The SML of 0.245 obtained from *Caiman sclerops* is intermediate between the values of 0.172 (Hernandez & Coulson, 1952) and 0.277 (Huggins, Hoff & Valentinuzzi, 1971) calculated from data previously presented on this species. Bennett & Dawson (1976) concluded on the basis of the available data that crocodilians possess metabolic levels similar to those of other orders of reptiles. In the present study it was found that *C. sclerops* possessed a SML at 30°C slightly higher than any of the lizard species examined. However, although the crocodilian SML was obtained under identical conditions to those of the lizards, it is possible that it does not represent a true basal level. Although Huggins, Hoff & Valentinuzzi (1971) reported oxygen consumption rates by *C. sclerops* corresponding to a metabolic level of 0.277 after a period of adjustment to the experimental chamber of about 30 minutes, this fell to 0.125 (Huggins, Valentinuzzi & Hoff, 1971) when the adjustment period was extended to 18 hours. Brown & Loveridge (1981) also found that the resting metabolic rate of *Crocodylus niloticus* decreased throughout 48 hours in an experimental chamber. Therefore, extremely long measurement periods, of greater duration than those adopted in the present study, may be required to determine the minimum oxygen consumption rates of these reptiles. It is possible that this ability to reduce their metabolism might be related to the diving physiology of crocodilians.

2.3.4 Summary

In the present study more than one representative of the four genera *Lacerta*, *Cordylus*, *Chalcides* and *Varanus* were examined. With the exception of *Chalcides*, the only genus within which there are also marked anatomical differences, SMLs appear relatively homogeneous, within these genera. Although the available data suggest that some families, such as the iguanids, scincids and gekkonids, are metabolically very diverse, others appear to be more conservative in the range of metabolic levels they encompass. However, it should be noted that in several of these families all the species so far examined belong to single genera. The differences in metabolic levels observed within and between families may not only be related to anatomical factors but also the result of adaptations to their thermal environment (see Chapter 6.4.2).

It is therefore apparent that the lizards cannot be regarded as a metabolically homogeneous group. Consequently any attempt to produce a single regression equation relating their metabolic rate to body mass would be inappropriate. However, it is possible to describe a metabolic band which encompasses the species included in the present study. For determinations at 30°C the lower limit of this band is given by the equation;

$$\text{SMR (ml } O_2\text{/h)} = 0.096.\text{Mass (g)}^{0.85}$$

and the upper limit by;

$$\text{SMR (ml } O_2\text{/h)} = 0.230.\text{Mass(g)}^{0.85}$$

The saurian metabolic band is therefore relatively broad, with some lizards possessing SMLs more than twice those of others. Future

work will probably result in a further widening of the band to accommodate species with even lower or higher SMLs. Including the data from the other studies listed in Table 2.8, which for the reasons already discussed are not strictly comparable, raises the upper limit of the band to;

$$\text{SMR (ml } O_2\text{/h)} = 0.321.\text{Mass (g)}^{0.85}$$

Because the lizards with the highest SMLs, such as *Chamaeleo* and *Anguis*, were not measured, the metabolic band at 37°C would be artificially narrow if defined only on the basis of the experimental data actually collected at this temperature. Therefore, although the lower limit has been taken directly from measurement at 37°C, the upper limit has been calculated from the 30°C data using the mean lizard Q_{10} value of 2.36. The resulting lower limit to the metabolic band at 37°C of the species examined in this study is therefore;

$$\text{SMR (ml } O_2\text{/h)} = 0.171.\text{Mass (g)}^{0.85}$$

and the upper limit;

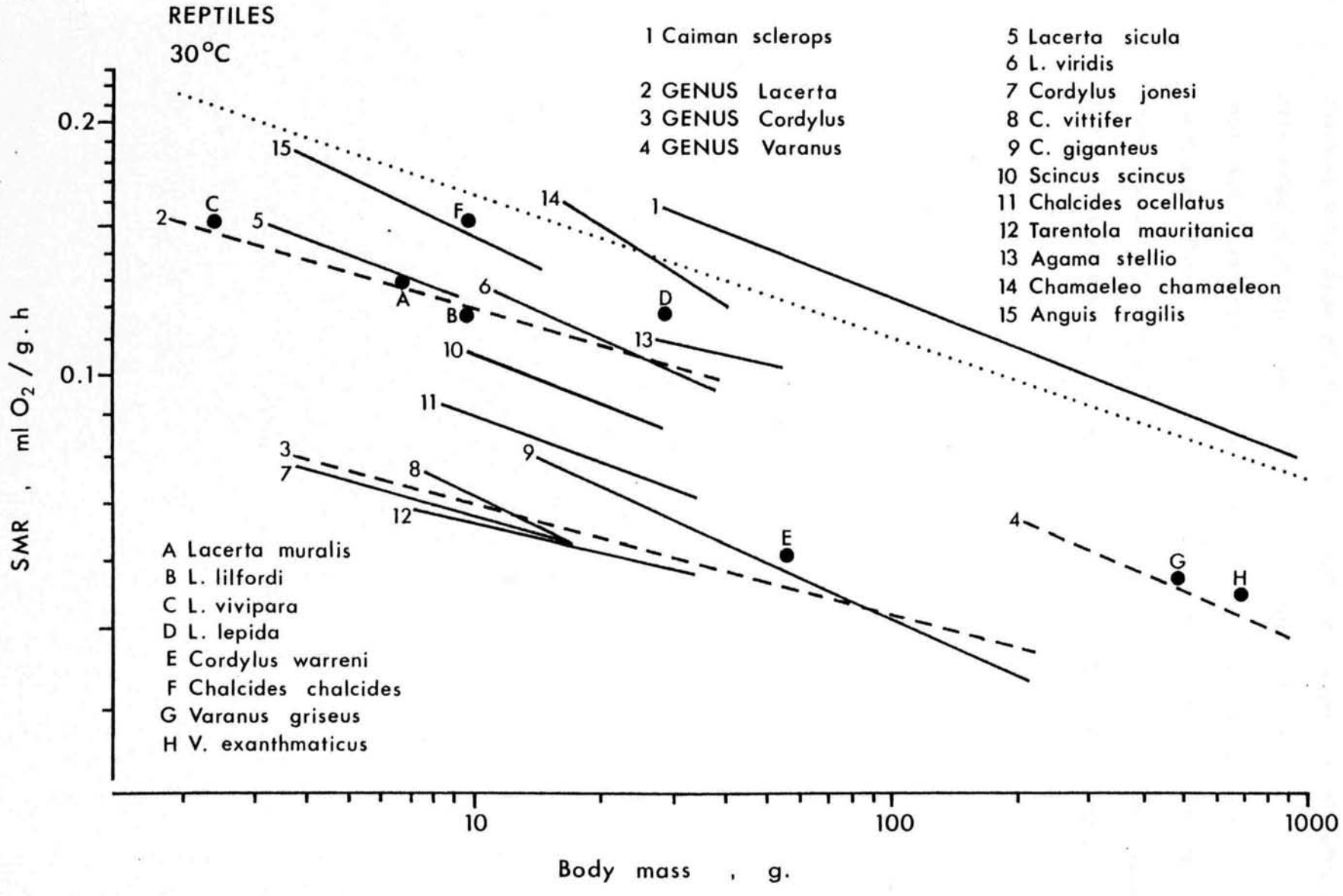
$$\text{SMR (ml } O_2\text{/h)} = 0.419.\text{Mass (g)}^{0.85}$$

However, as already discussed, it is possible that the exponent may be slightly lower at this higher temperature.

The general regression equations produced by Bennett & Dawson (1976) lie close to the upper limits of these bands (Fig. 2.31). One of the reasons for this is that low SMLs are more common among lizards than was once appreciated and cordylids, gekkonids and xantusids, the families currently defining the lower limit of the saurian metabolic band, were very poorly represented in the data used by Bennett &

Figure 2.31 Summary diagram of the relationships between standard metabolic rate (SMR) at 30°C and body mass in lizards and crocodilians. Regression lines (see Tables 2.2 and 2.4) extend across the body mass range over which they were determined. Points are plotted at the mean SMRs and body masses of species from which less extensive data were obtained (see Table 2.3). The dotted line is that produced by Bennett & Dawson (1976), $SMR = 0.240.Mass^{0.83}$, for lizards at 30°C.

Fig. 2.31


REPTILES
30°C
1 Caiman sclerops
2 GENUS Lacerta
3 GENUS Cordylus
4 GENUS Varanus
5 Lacerta sicula
6 L. viridis
7 Cordylus jonesi
8 C. vittifer
9 C. giganteus
10 Scincus scincus
11 Chalcides ocellatus
12 Tarentola mauritanica
13 Agama stellio
14 Chamaeleo chamaeleon
15 Anguis fragilis
A Lacerta muralis
B L. lilfordi
C L. vivipara
D L. lepida
E Cordylus warreni
F Chalcides chalcides
G Varanus griseus
H V. exanthmaticus
SMR , ml O2 / g . h
0.2
0.1
10
100
1000
Body mass , g.

Dawson (1976). This was biased towards iguanids and scincids, two families which apparently include a significant proportion of species with relatively high metabolic levels. However, it would be desirable to re-examine some of these lizards under the standard conditions adopted in the present study to establish the extent to which these higher oxygen consumption rates represent real metabolic differences or result from variations in measurement procedures.

CHAPTER 3

THE BASAL METABOLIC LEVELS (BMLs) OF EUTHERIAN MAMMALS

3.1 INTRODUCTION

The next objective of the study was to quantify the extent of the difference between the BMLs of mammals and the SMLs of reptiles at 37°C. Far more comparative work has already been conducted on mammals than reptiles, and consequently more data on their BMRs is available in the existing literature. Several workers have produced general regression equations relating BMR to body mass in eutherian mammals, and these show good agreement with one another. The most frequently used of these include:

$$\text{BMR (ml } O_2\text{/h)} = 3.441 \text{ Mass (g)}^{0.734} \quad \text{Brody (1945)}$$

$$\text{BMR (ml } O_2\text{/h)} = 3.417 \text{ Mass (g)}^{0.75} \quad \text{Kleiber (1961)}$$

$$\text{BMR (ml } O_2\text{/h)} = 3.800 \text{ Mass (g)}^{0.75} \quad \text{Schmidt-Nielsen (1975)}$$

It has been previously recognised that the living eutherian mammals are not a completely metabolically homogeneous group and some taxa, notably microchiropterans, small insectivores and mustelids, may deviate from these general relationships (Poczopko, 1071; McNab, 1974). In addition both the monotremes (Hulbert, 1980) and marsupials (MacMillan & Nelson, 1969; Dawson & Hulbert, 1970) possess lower BMLs than eutherian mammals.

In view of this large amount of existing information, the aim of the present study was not to undertake a comprehensive examination of mammalian metabolic levels but to obtain sufficient data, using standardised procedures and techniques, to allow accurate comparisons to be made with reptiles. Also good agreement between mammalian

measurements from this study and those in the established literature would provide additional confirmation that the techniques used were giving accurate determinations of oxygen consumption rates. This will increase the confidence which can be placed in the values obtained from other species, particularly many of the reptiles, for which there is no previous literature.

The majority of this study concentrated on rodents as a selection of species, both of wild and laboratory-bred strains, was available covering a similar body mass range to that of the reptiles examined. Also, the existing literature indicates that rodents are fairly typical mammals with regard to their metabolic levels. In addition a few representatives of groups known to possess different BMLs were also examined. These consisted of a mustelid carnivore *Mustela nivalis*, a microchiropteran bat *Pipistrellus pipistrellus* and two small insectivores *Sorex araneus* and *S. minutus*. Although most studies have found that shrews possess metabolic levels higher than those of other eutherian mammals, Hawkins, Jewell & Tomlinson (1960) and Hawkins & Jewell (1962) claimed that the metabolic rates of *S. araneus* and *S. minutus* are no different to those of rodents of similar body mass. It was therefore decided to undertake a detailed examination of these two species across the range of measurement temperatures used by the earlier studies.

3.2 MATERIALS AND METHODS

3.2.1 Animals

Sources

Laboratory-bred mice *Mus musculus* and rats *Rattus norvegicus* were taken from colonies maintained at the University of Durham. Wild rodents and shrews were obtained with Longworth traps from hedgerows and woodlands in the Durham City area during the late spring and summer. The species used were the long-tailed field mouse *Apodemus sylvaticus*, bank vole *Clethrionomys glareolus*, common shrew *Sorex araneus* and pigmy shrew *S. minutus*. Some of the *Clethrionomys* were laboratory-bred offspring of wild-caught parents. Wild house mice *Mus musculus* were obtained using Longworth traps in various buildings in the area. Pipistrelle bats *Pipistrellus pipistrellus* were caught with a hand net as they emerged from a roost in County Durham. All the weasels *Mustela nivalis* used in this study were captive bred individuals.

Maintenance

Laboratory mice and rats were maintained in small groups under normal animal house conditions. They were fed on rodent pellets and drinking water was freely available at all times. The temperature of the animal rooms was approximately 20°C and a 12 L:12 D photoperiod was maintained, the photophase commencing at 08.00 GMT. Wild-caught rodents were kept in the laboratory in rodent cages containing peat or sawdust substrate, with hay or shredded paper bedding. Their diet consisted primarily of grain and rodent pellets with some fresh green-food.

Shrews were housed individually in 34 x 24 x 20 cm plastic tanks. These contained a deep 5-8 cm layer of dried peat, and hay was provided

for the animals to construct nests. Both peat and bedding were changed every two days. They were fed a mixed diet of live invertebrates, consisting principally of locusts, *Tenebrio* and *Calliphora* larvae and earthworms. The shrews required feeding at frequent intervals, but care was needed to prevent overfeeding, leading to excessive weight gain. Although previous work (Illman, 1974) had suggested that these mammals are very difficult to maintain in captivity, no problems were experienced during this study, with the exception of some mortality during the initial trapping. Some individuals were kept for more than three months, during which time they became exceptionally tame.

Pipistrelles were kept in small covered plastic tanks, the sides of which were fitted with sheets of thick foam rubber for the bats to hang from. The tanks were placed in a dark cupboard where they received minimal disturbance. They were fed primarily on *Tenebrio* larvae and water was provided, although they were never seen to drink.

Each weasel was housed individually in a stainless steel tank, measuring approximately 120 x 60 x 30 cm, fitted with a wire mesh top. The tanks contained a thick layer of dried peat on which were placed small branches and dried leaves. The cages had detachable nest boxes with hay bedding. The diet of the weasels consisted of dead mice, rats and chicks supplemented with vitamins.

3.2.2 Determination of basal metabolic rate (BMR)

Mammalian oxygen consumption rates were measured using the same equipment described in Chapter 2.2.2 for determining the SMRs of reptiles. Any differences in the procedures used are discussed below.

3.2.3 Experimental procedures

Wild-caught mammals were maintained in the laboratory, at a temperature of approximately 20°C, for a minimum of 4 weeks before the start of experiments. However, bats could not be satisfactorily kept in the laboratory for long periods and were only held for 1 week before measurements commenced.

Due to their higher metabolic level mammals attain a post-absorptive state sooner after feeding than do reptiles. Therefore, the period for which food was withheld before animals were placed in the measurement chamber was shorter. Larger rodents were fasted for 24 hours, and weasels, bats and small rodents for 12 hours. Shrews cannot tolerate long periods without food and could only be safely fasted for 1 hour before experiments.

Determinations of oxygen consumption rates were made in a darkened chamber during the animal's photophase. The chambers contained a layer of sawdust or filter paper to absorb any urine excreted and prevent this soiling the fur and reducing the animal's thermal conductance. The higher metabolic levels of mammals required faster flow rates of air through the apparatus than were used with reptiles. To prevent significant changes in oxygen or carbon dioxide concentrations in the chamber flow rates ranged from approximately 25 to 250 ml/min, for small bats and weasels respectively. Oxygen uptake by individual mammals was usually monitored continuously for 6 to 8 hours. This period is too long for shrews to be kept without access to food, and therefore these mammals were only placed in the chamber for about 3 hours. Animals were weighed immediately before and after each experiment and the mean value used in further calculations.

As measurements of BMR were wanted, the temperature of the chamber

was within the thermoneutral zone of each mammal. Usually environmental temperatures of 34 to 36°C were used for small voles, mice and bats, and slightly lower temperatures of 32 to 34°C for larger species like weasels and rats. These temperature were established in preliminary experiments in which the chamber temperature was gradually raised until a SMR was obtained which was not reduced by further increases in environmental temperature. The SMRs of shrews were determined across a wide range of environmental temperatures from 0°C to conditions of thermoneutrality.

The statistical analysis of the results was as previously described in Chapter 2.2.4.

3.3 RESULTS AND DISCUSSION

3.3.1 Determinations of basal metabolic rate (BMR)

The BMRs of a total of 8 mammal species were determined. Sufficient measurements were obtained from domestic *Mus musculus*, *Apodemus sylvaticus* and *Rattus norvegicus* for the relationship between BMR and body mass to be examined intra-specifically. Regression equations were also produced for domestic *Mus musculus* and *Rattus norvegicus* from the data relating to adult animals only. An intra-generic exponent for the genus *Sorex* and general exponents for rodents were also calculated by regressing together all the individual BMR measurements of their respective member species. All the data from rodents and shrews is presented graphically in Figs. 3.1 to 3.3 and the regression parameters summarised in Table 3.1. All intra-specific, intra-generic and general relationships between both total and mass specific BMR and body size are significant ($p < 0.05$), with the exception of those relating to the mass specific BMR of adult animals only in *Mus musculus* and *Rattus norvegicus*. The mean BMRs of 6 species, from which insufficient data were obtained to calculate intra-specific exponents, are given in Table 3.2.

The influence of environmental temperature (T_e) on the SMR of 3 *Sorex araneus* and 2 *Sorex minutus* are shown in Fig. 3.4. The minimum thermal conductance of each shrew, calculated by linear regression of SMR measurements below the lower critical temperature (T_{lc}) against T_e (see Chapter 1.3) are presented in Table 3.3. Considerable confidence can be attached to the thermal conductances obtained since the regression equations extrapolate on the abscissa to temperatures in the range 36.7-42.7°C, which are close to the body temperatures

Table 3.1 Regression parameters of the relationship between basal metabolic rate (BMR) and body mass for mammals

Species		n	Body mass, g range (mean)	Intercept, a	Exponent, b, ± 95% confidence limits Total (Mass specific)	r
Apodemus sylvaticus		20	16.4-26.2 (21.9)	5.462	0.57 ± 0.20*	0.81
					(-0.43 ± 0.20*)	
Mus musculus	ALL	52	8.0-38.2 (19.9)	6.322	0.55 ± 0.06*	0.93
(domestic)					(-0.45 ± 0.06*)	
	ADULT, > 20 g	18	20.2-38.2 (28.7)		0.78 ± 0.28*	0.83
					(-0.22 ± 0.28)	
Rattus norvegicus	ALL	26	29.9-425 (136.5)	6.001	0.65 ± 0.04*	0.99
(domestic)					(-0.35 ± 0.04*)	
	ADULT, > 100 g	10	118-425 (288)		0.82 ± 0.19*)	0.96
					(-0.18 ± 0.19)	

Table 3.1 continued

Species		n	Body mass, g range (mean)	Intercept, a	Exponent, b, ± 95% confidence limits Total (Mass specific)	r
RODENTS	ALL	114	8.0-425 (45.9)	3.766	0.73 ± 0.03*	0.98
					(-0.27 ± 0.03*)	
	ADULT	44	15.6-425 (85.3)	2.801	0.78 ± 0.03*	0.99
					(-0.22 ± 0.03*)	
GENUS Sorex		21	3.6-12.4 (8.0)	14.557	0.55 ± 0.05*	0.98
					(-0.45 ± 0.05*)	

*$p < 0.05$

Figure 3.1 Relationship of total basal metabolic rate to body mass for rodents. The solid line was fitted by linear regression analysis to all the data and the broken line to measurements of adult mammals only.

Figure 3.2 Relationship of mass specific basal metabolic rate to body mass for rodents. For key see Fig. 3.1.

Fig. 3.1

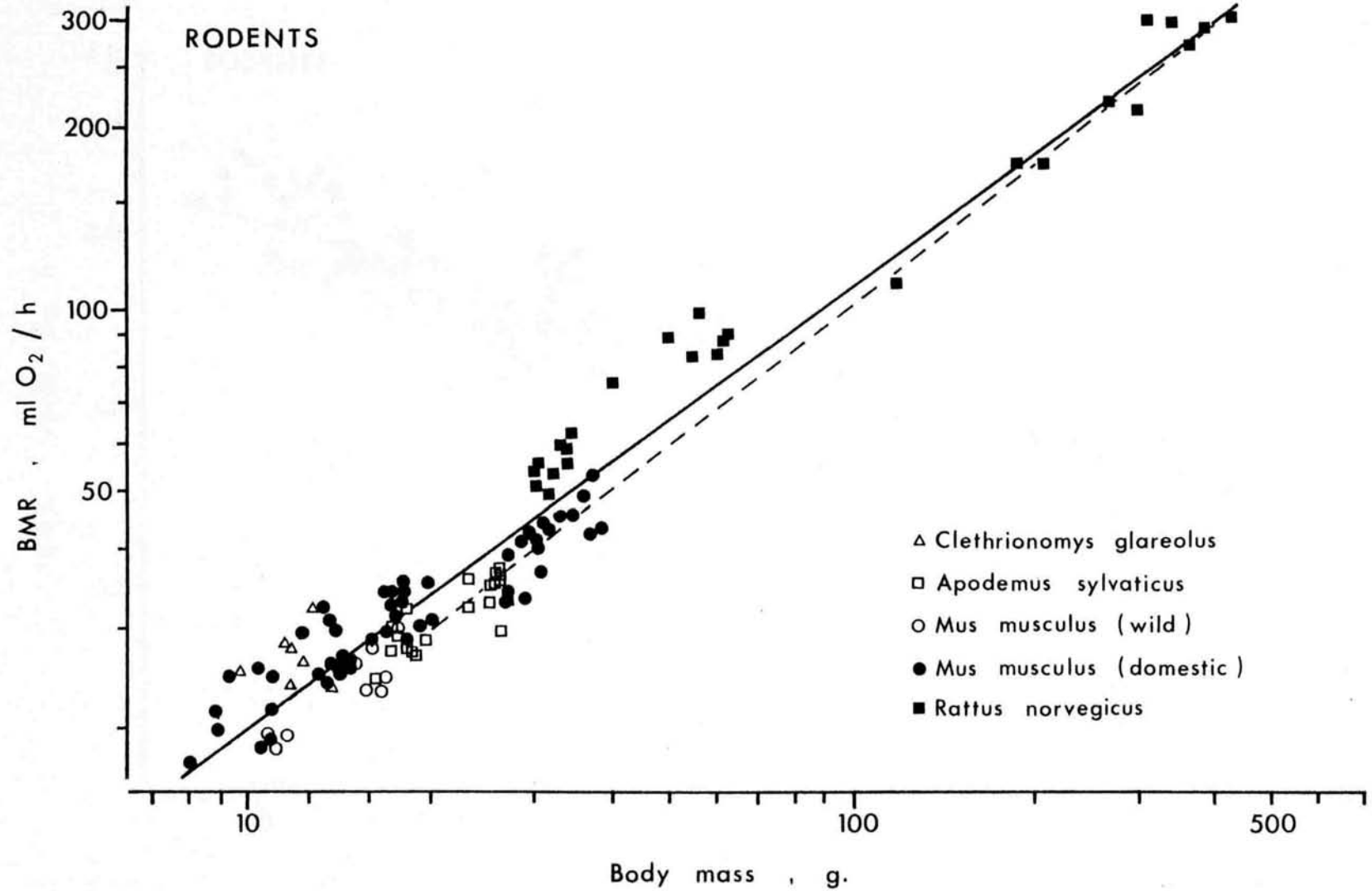

RODENTS
300
200
100
50
BMR , ml O_2 / h
10
100
500
Body mass , g.
Clethrionomys glareolus
Apodemus sylvaticus
Mus musculus (wild)
Mus musculus (domestic)
Rattus norvegicus

Fig. 3.2

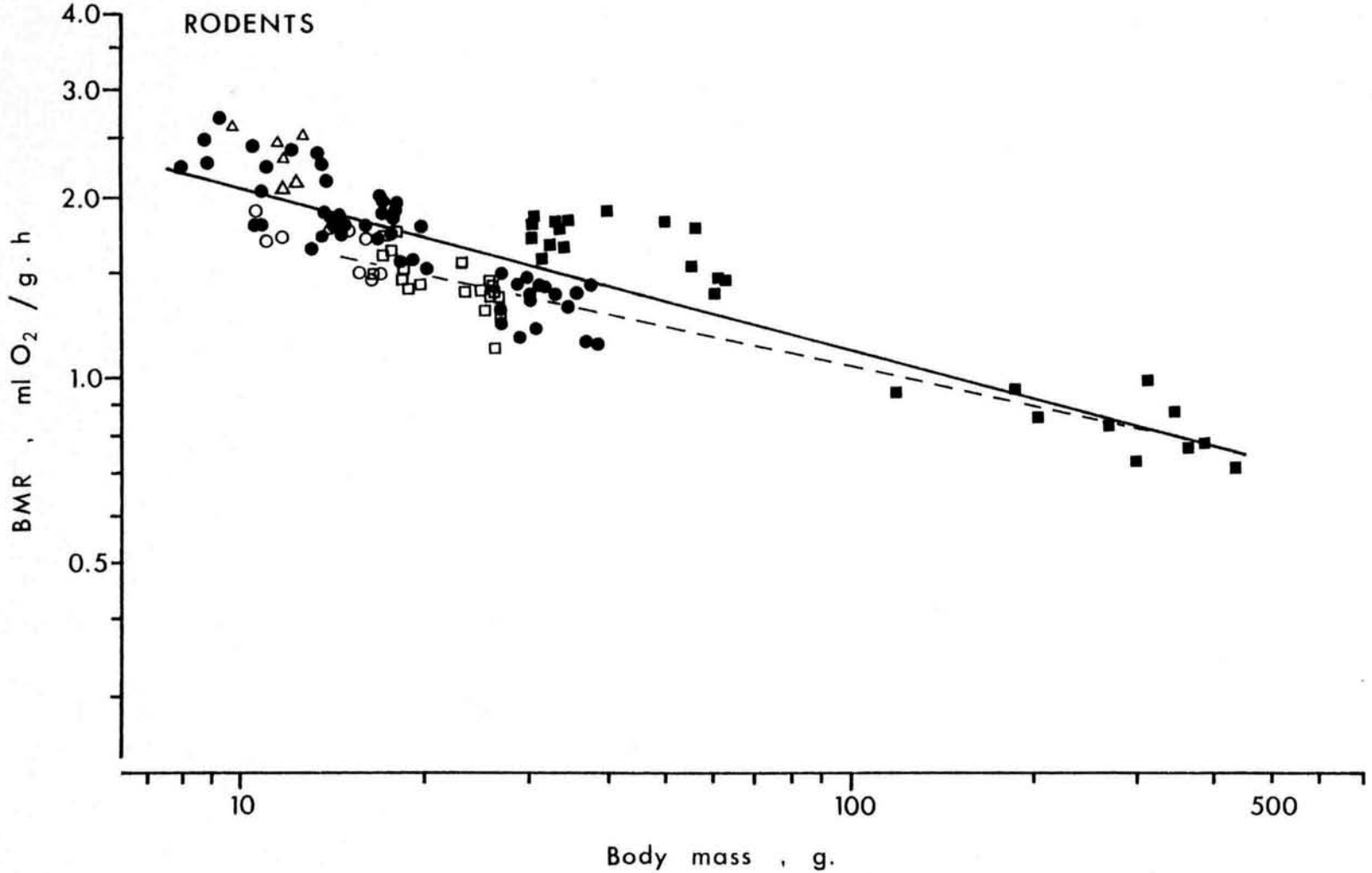


Figure 3.3 Relationships of (a) total and (b) mass specific basal metabolic rate to body mass for shrews of the genus *Sorex*. Lines were fitted by linear regression analysis.

Fig. 3.3

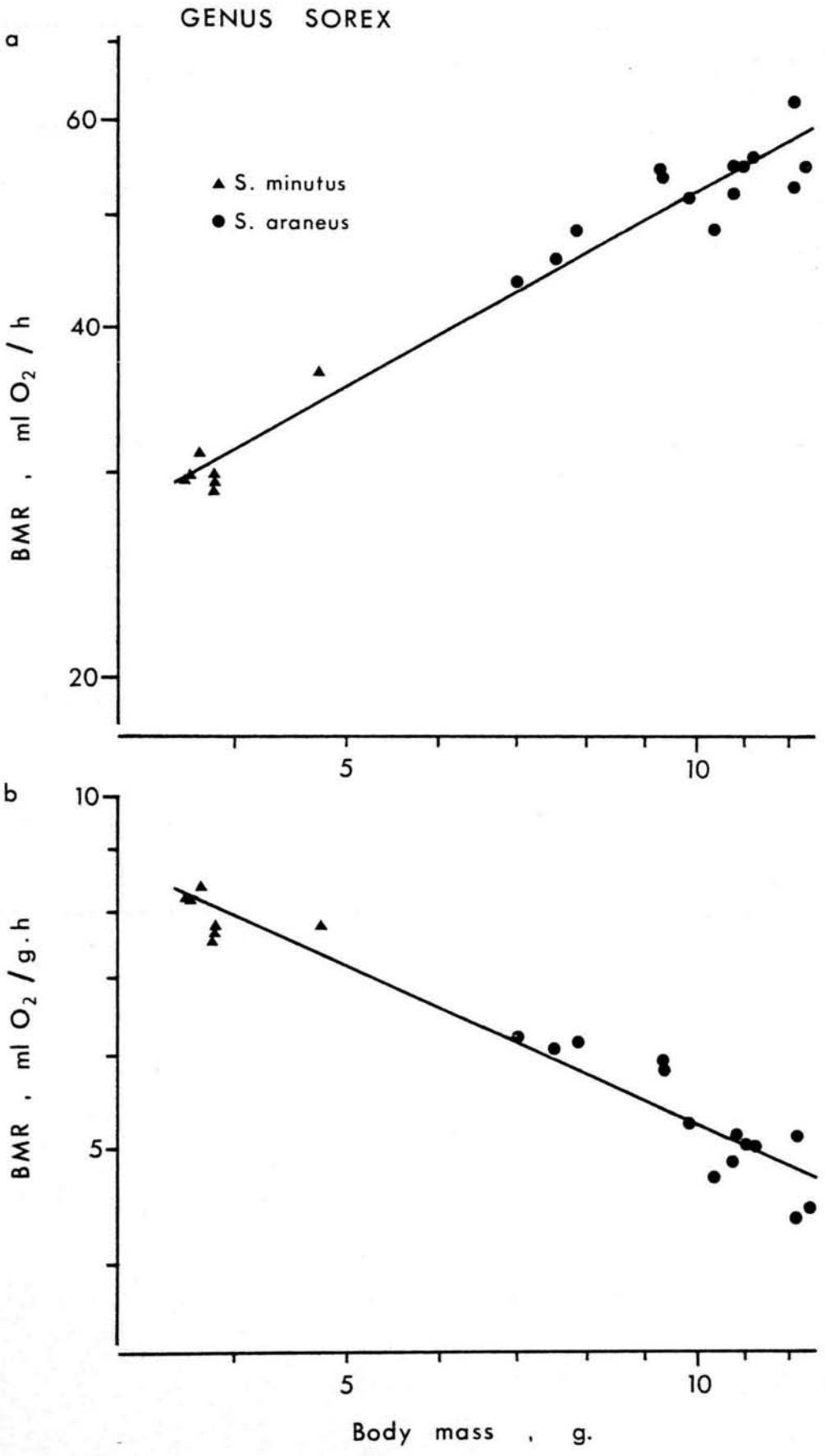

GENUS SOREX
a
60
40
20
▲ S. minutus
● S. araneus
BMR , ml O_2 / h
5
10
b
10
5
BMR , ml O_2 / g.h
5
10
Body mass , g.

Table 3.2 Basal metabolic rates (BMRs) of mammals

Species	n	Body mass, g. mean (range)	BMR, mean ± SE ml O_2/h ($ml\ O_2/g.h$)
Clethrionomys glareolus	7	11.8 (9.7-13.2)	26.52 ± 1.10 (2.26 ± 0.11)
Mus musculus (wild)	9	14.5 (10.7-17.3)	24.15 ± 1.50 (1.68 ± 0.06)
Sorex minutus	7	3.9 (3.6-4.7)	30.68 ± 1.02 (7.91 ± 0.11)
Sorex araneus	14	10.1 (7.0-12.4)	52.47 ± 1.29 (5.29 ± 0.17)
Pipistrellus pipistrellus	20	4.9 (3.7-6.6)	6.88 ± 0.14 (1.41 ± 0.03)
Mustela nivalis	6	102 (82.2-132)	182.6 ± 12.9 (1.80 ± 0.05)

Figure 3.4 The influence of environmental temperature on the standard metabolic rates of two *Sorex minutus* and three *S. araneus*. Lines were fitted to the measurements made below the thermoneutral zone of each shrew by linear regression analysis. The slopes of these lines, which describe the minimum thermal conductances of the animals, are given in Table 3.3.

Fig. 3.4

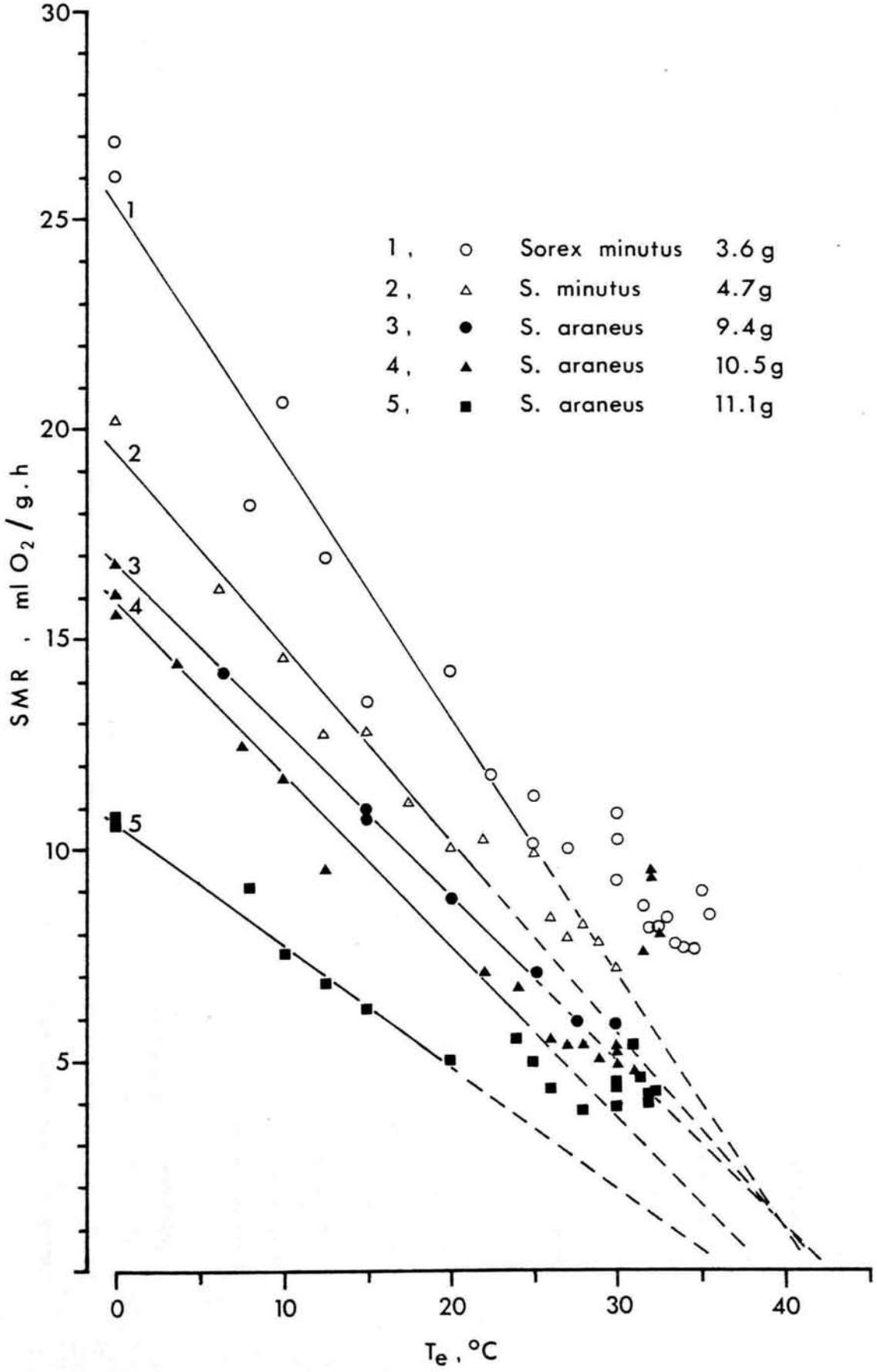

30
25
20
15
10
5
0
10
20
30
40
SMR . ml O_2 / g.h
T_e , °C
1 , ○ Sorex minutus 3.6 g
2 , △ S. minutus 4.7g
3 , ● S. araneus 9.4g
4 , ▲ S. araneus 10.5g
5 , ■ S. araneus 11.1g
1
2
3
4
5

Table 3.3 Minimum thermal conductances of small insectivores of the genus *Sorex*

Species	Body mass, g mean	Minimum thermal conductance, ml O_2/g.h.°C			Intercept on abscissa,°C
		Measured (± 95% c.l., n)	Predicted		
			Herreid & Kessel, 1967	Bradley & Deavers, 1980	
Sorex minutus	3.6	0.614 (± 0.129, 10)	0.536	0.440	41.5
Sorex minutus	4.7	0.461 (± 0.084, 8)	0.468	0.393	42.2
Sorex araneus	9.4	0.392 (± 0.036, 5)	0.330	0.293	42.7
Sorex araneus	10.5	0.410 (± 0.059, 9)	0.312	0.279	38.7
Sorex araneus	11.1	0.291 (± 0.054, 7)	0.303	0.273	36.7
Sorex cinereus (Morrison et al, 1959)	3.5	0.59	0.543	0.446	
Sorex minutus (Gebczynski, 1971)	4.6	0.56	0.473	0.397	
Sorex araneus (Gebczynski, 1965)	7.6	0.53	0.367	0.320	

previously reported for these small insectivores (Morrison, Ryser & Dawe, 1959).

3.3.2 Relationships between BMR and body mass in eutherian mammals

It has long been known that mammalian BMRs are allometrically related to body mass by an exponent of less than the unity required for a simple mass dependency. Attempts have been made to relate BMR to the surface area of the animal from which heat is lost, the so-called 'surface rule'. If BMR is surface area dependent an exponent of 0.67 would be expected (Meeh, 1879; Lambert & Teissier, 1927). However, calculations of the inter-specific exponent from experimental data have produced values intermediate to 0.67 and the 1.00 required for mass dependency. Combining measurements of BMR from 10 groups of mammals, Kleiber (1932) produced an exponent of 0.739, a value later revised to 0.756 (Kleiber, 1947) when recalculated from a larger data set of 26 groups. Benedict (1938) found a similar value of 0.75, although Brody & Procter (1932) produced a slightly lower exponent of 0.734. Currently body mass raised to the power of 0.75 is generally aecepted as the reference base for comparisons of basal metabolic level (BML) between mammals of differing body mass (Kleiber, 1961; Harris, 1966; Bligh & Johnson, 1973). No attempt was made to calculate a general exponent from all the mammalian data gathered in the present study, since more than a single metabolic level is clearly represented. The exponents calculated from all the measurements of rodent metabolism, and those relating to adults only, are 0.73 and 0.78, respectively, and therefore in good agreement with a value of 0.75.

Intra-specific exponents were found to be lower than the general mammalian value. *Mus musculus* and *Rattus norvegicus* produced overall

exponents of 0.55 and 0.65, respectively, which are both significantly lower than 0.75 ($p < 0.001$). These results are similar to those obtained by Heusner (1982) from an analysis of metabolic data from seven species of mature mammals. This produced a general exponent of 0.776 when the data from all species were regressed together, a value similar to that of 0.78 from adult rodents in the present study. However, within species the exponents averaged 0.67, and none of the values were significantly different from that predicted by the 'surface rule' theory.

A possible reason for these lower intraspecific exponents is that within smaller taxonomic groupings, within which animals are more uniform in their body form and thermal environment, BMR is more closely related to surface area to volume ratio. However, the intra-specific exponents of *Mus musculus* and *Apodemus sylvaticus*, and the intra-generic exponent of *Sorex*, are even lower than 0.67. This could be because factors other than surface area, such as the amount of superficial insulation and sub-cutaneous fat, are influencing heat loss. Inter-specific analyses have produced exponents for minimum total thermal conductance among mammals of 0.495 (Herreid & Kessel, 1967) and 0.574 (Bradley & Deavers, 1980), values less than 0.67 and similar to the lower intra-specific and intra-generic BMR exponents calculated here. However, there is no obvious theoretical reason why there should be a close relationship between BMR and thermal conductance because under natural conditions many mammals experience temperatures below thermoneutrality, and therefore BMR will only constitute one component of their total resting endogenous heat production. Also arguments based on thermal exchange with the environment do not explain why

intra-specific values are also lower than the general exponent in reptiles (Chapter 2.3.2).

Another explanation for the reduced exponents within species could be that the smaller animals represented are younger individuals, the BMRs of which will be increased by the energetic demands of biosynthesis and growth. This factor may have contributed to the low overall exponent of 0.55 for *Mus musculus*, as when the analysis was confined to adult animals, weighing more than 20 g, a value of 0.78 was produced. However, it cannot account for the low mean intra-specific exponent calculated by Heusner (1982), or that produced for the genus *Sorex* in the present study, since these were calculated from measurements of mature animals.

3.3.3 The basal metabolic levels (BMLs) of eutherian mammals

The basal metabolic level (BML) of each species was determined using a general exponent of 0.75 (Table 3.4). Composite BMLs were also produced for rodents and insectivores of the genus *Sorex*. Because intra-specific exponents are significantly lower than 0.75, separate BMLs were also calculated from the data relating to adult mammals only. All values are the means of the appropriate BML estimates calculated from the individual measurements of total metabolic rate using the equation:

$$BML = \frac{BMR\ (ml\ O_2/h)}{Mass\ (g)^{0.75}}$$

The 4 species of rodents examined possessed similar BMLs, with the exception of *Clethrionomys glareolus*. However, the higher metabolic level of 4.182 obtained from this species is probably because all the individuals used were young animals, since the mean BML of immature

Table 3.4 Basal metabolic levels (BMLs) of mammals calculated using a general exponent of 0.75.

Species		BML, mean (± SE,n)
Rodentia		
Clethrionomys glareolus	YOUNG	4.182 (± 0.187, 7)
Apodemus sylvaticus	ALL	3.129 (± 0.054, 20)
	ADULT, > 20 g	3.062 (± 0.071, 11)
Mus musculus (wild)	ALL	3.258 (± 0.106, 9)
	ADULT, > 15 g	3.250 (± 0.189, 5)
Mus musculus (domestic)	ALL	3.560 (± 0.065, 52)
	ADULT, > 20 g	3.148 (± 0.058, 18)
Rattus norvegicus (domestic)	ALL	3.911 (± 0.101, 26)
	ADULT, > 100 g	3.405 (± 0.105, 10)
RODENTS	ALL	3.579 (± 0.051 114)
	ADULT	3.197 (± 0.046 44)
Insectivora		
Sorex minutus		11.096 (± 0.148, 7)
Sorex araneus		9.358 (± 0.204, 14)
GENUS Sorex		9.938 (± 0.232, 21)

Table 3.4 (continued)

Species	BML, mean (± SE,n)
Chiroptera	
Pipistrellus pipistrellus	2.108 (± 0.029, 20)
Carnivora	
Mustela nivalis	5.702 (± 0.162, 6)

domestic mice weighing less than 10 g is a comparable value of 4.163. The BMLs of adult domestic *Mus musculus*, 3.148, and *Rattus norvegicus*, 3.405, are similar to those reported for these species by Morrison (1948) of 3.330 and 3.250, respectively. Domestic *Mus musculus* possessed a BML not significantly different from the 3.250 obtained from wild-caught animals. The overall mean BML for adult rodents of 3.197 is very close to a value of 3.249 calculated from data on ten species by Poczopko (1971). Rodents therefore appear to be a metabolically typical group of mammals, since these values are close to those associated with the general equations relating BMR to body mass in eutherian mammals produced by Brody (1945) and Kleiber (1961) of 3.441 and 3.417, respectively.

Many chiropterans have been found to possess metabolic levels lower than those of other eutherian mammals (Morrison, 1948; Poczopko, 1971). However, care must be taken when comparing the metabolism of bats with other groups of mammals since many smaller species are poor thermoregulators and may enter periods of torpor while inactive (Henshaw, 1970). The BML obtained from *Pipistrellus pipistrellus* of 2.108 is comparable to a mean value of 2.606 for nine other species of microchiropterans (Poczopko, 1971), and only 0.7 times that of adult rodents.

In contrast, the BML of *Mustela nivalis* of 5.702 is 1.8 times the mean value of adult rodents. This is consistent with earlier findings that the metabolic levels of mustelid carnivores, particularly smaller species weighing less than 1 kg, are relatively high (Scholander *et al*, 1950; Iversen, 1972). Although lower than the value of 7.411 predicted for 100 g weasels by the regression equation of Iversen (1972), the BML produced for this species in the present study is within the range of

values previously reported for other members of the genus *Mustela* (Brown & Lasiewski, 1972; Casey, Withers & Casey, 1979; Korhonen, Hari & Asikainen, 1983). These elevated metabolic levels of small mustelids are thought to be related to their relatively high thermal conductances, which are a consequence of their elongate body form (Iversen, 1972).

The BML of 9.358 obtained from the shrew *Sorex araneus* is intermediate to values of 7.761 and 12.935, calculated from data presented by Hawkins, Jewell & Tomlinson (1960) and Gebczynski (1965), respectively. *S. minutus* was found to have a BML of 11.096, comparable to that previously reported for this species by Hawkins, Jewell & Tomlinson (1960) of 11.131. These metabolic levels are lower than those calculated from data on both species presented by Vogel (1976). However, those were obtained during very short measurement periods from animals at 25°C, a temperature below thermoneutrality for smaller shrews (see Fig. 3.4). It is generally recognised that small insectivores possess considerably higher metabolic rates than those of other eutherian mammals extrapolated to a similar body mass (Morrison, 1948; Morrison, Ryser & Dawe, 1959; Gebczynski, 1965, 1971); Vogel, 1976), and in the present study the mean BML of the genus *Sorex* was 3.1 times that calculated for adult rodents.

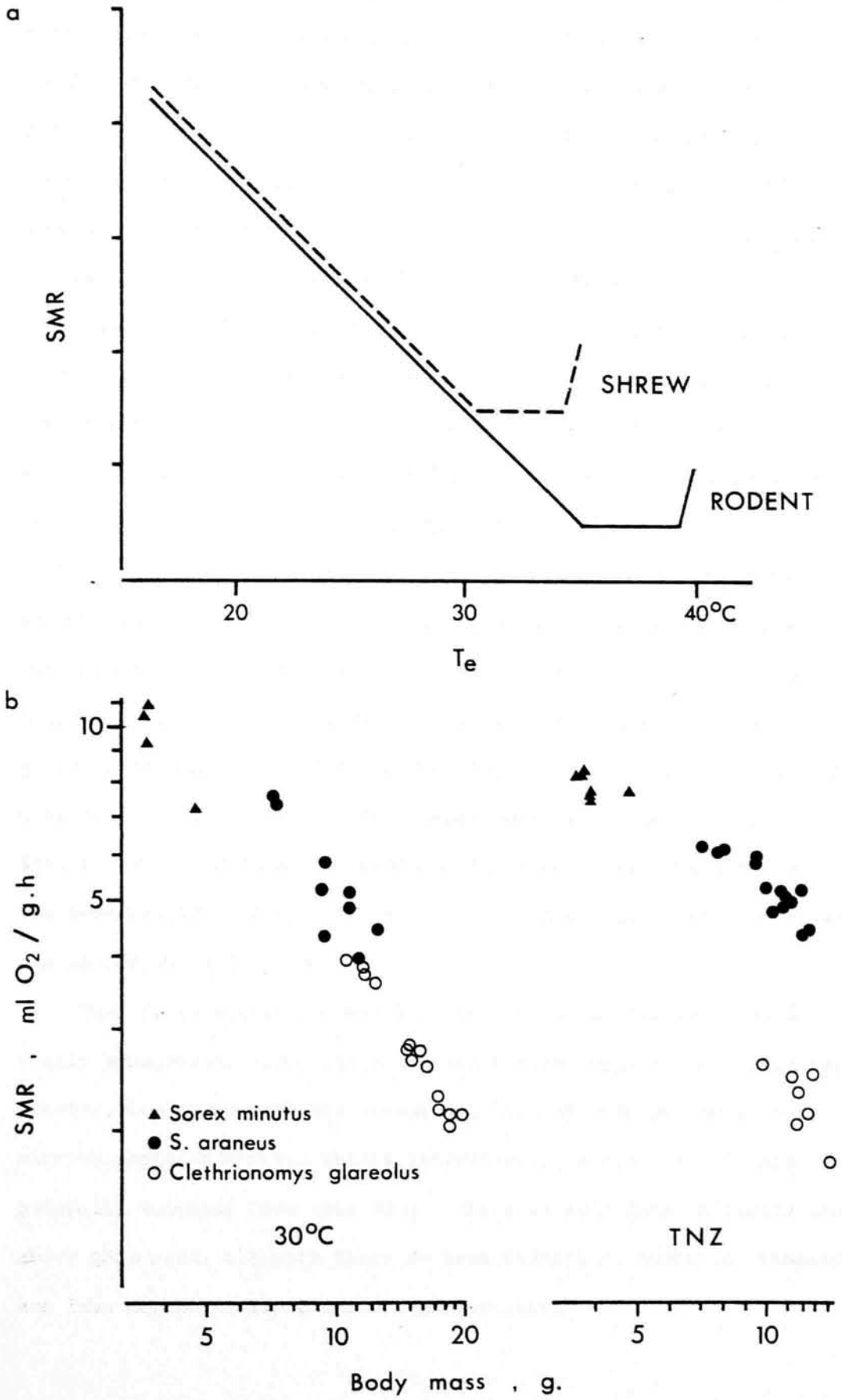
However, Hawkins, Jewell & Tomlinson (1960) and Hawkins & Jewell (1962) have claimed that the metabolic rates of *S. araneus* and *S. minutus* are little different from those of small rodents. The reason for this discrepancy could be that these two studies were not comparing both groups under conditions of thermoneutrality and at lower temperatures the measured metabolic rate reflects the thermal conductance of the mammal rather than its BML (see Chapter 1.3). The

thermal conductances obtained in the present study are comparable to those calculated from data previously presented for shrews of the genus *Sorex*, and those predicted by the general equations of Herreid & Kessel (1967) and Bradley & Deavers (1980) relating conductance to body mass in mammals (Table 3.3). Therefore, unlike mustelids, the elevated BMLs of shrews cannot be attributed to a high thermal conductance. Because shrews and small rodents possess comparable body temperatures and thermal conductances, at temperatures below the thermoneutral zone of both groups their endogenous heat production will be similar (Fig. 3.5a). Since the BMLs of shrews are higher they will attain thermoneutrality at lower environmental temperatures than rodents of similar body mass. However, the combination of a typical thermal conductance and an increased minimum level of endogenous heat production will reduce both the lower (T_{lc}) and upper (T_{uc}) critical temperatures, and therefore shrews will be more vulnerable to hyperthermia than rodents. Above the T_{uc} the temperature gradient between the animal and its surroundings is insufficient to allow adequate dissipation of even its basal metabolic heat production. As a consequence of the resulting heat storage, body temperature will start to rise, eventually causing death. In preliminary experiments of the present study two *S. araneus* were accidentally killed by exposure to environmental temperatures of 30 to 32°C for less than one hour. Platt (1974) found in the larger species *Blarina brevicauda*, weighing approximately 21.0 g, that environmental temperatures as low as 25°C caused elevations in body temperature of inactive shrews and animals died from hyperthermia at 30-35°C, depending on the relative humidity. Morrison, Ryser & Dawe (1959) reported a T_{uc} for *Sorex cinerus* of only 30.5°C. Consequently, the T_{uc} of shrews is lower than even the T_{lc} of many small rodents.

Figure 3.5 (a) Schematic diagram of the influence of environmental temperature on the standard metabolic rate of a shrew and small rodent with the same body mass. (For explanation see text 3.3.3).

(b) Comparisons of the standard metabolic rates of shrews of the genus *Sorex* and the small rodent *Clethrionomys glareolus* at an environmental temperature of 30 °C and under the appropriate conditions of thermoneutrality for each animal.

Fig. 3.5


a
SMR
SHREW
RODENT
20
30
40°C
Te
b
SMR , ml O2 / g.h
10
5
▲ Sorex minutus
● S. araneus
○ Clethrionomys glareolus
30°C
TNZ
5
10
20
5
10
Body mass , g.

Therefore, when compared under conditions of thermoneutrality shrews have BMLs considerably higher than rodents. However, this difference is of little energetic significance to animals living under natural conditions in cool temperate environments where they will normally be below their T_{lc}. Consequently, wild shrews probably have energetic demands similar to those of other small mammals. This probably explains why Hawkins & Jewell (1962) found little difference between the calorific requirements of various insectivores and rodents, assessed by measuring food intake, at environmental temperatures of 10 to 23°C. Hawkins, Jewell & Tomlinson (1960) also reported that the metabolic rates of shrews were no higher than those of similarly sized mice when compared in a differential calorimeter at 28 to 30°C. Although at this temperature the shrews will have been in a state of thermoneutrality, the small rodents were almost certainly below their T_{lc} and consequently their metabolic rates would have been elevated above the basal level. In the present study it was found that there is little difference between the resting metabolic rates of the genus *Sorex* and young voles *Clethrionomys glareolus*, of similar body mass to the larger shrews, when comparisons were made at 30°C. However, when the metabolic rates of the rodents were measured at thermoneutrality, 34 to 35°C, they were considerably less than those of the insectivores (Fig. 3.5b).

Therefore, eutherian mammals, like reptiles, are not a metaboli-
-cally homogeneous group and encompass a wide range of metabolic levels. However, the forms with the lowest and highest recorded BMLs, the microchiropteran bats and shrews respectively, are all small animals, generally weighing less than 25 g. The available data indicates that above this mass, although there is some variation, eutherian mammals are less metabolically diverse than reptiles.

3.3.4 Differences in the metabolic levels of reptiles and eutherian mammals

Several previous studies have commented on the extent of the differences between the metabolic rates of similarly sized reptiles and higher vertebrates. However, most of these compared data from reptiles with that produced by independent studies of mammals. Very few have made direct comparisons of reptilian and mammalian measurements obtained using the same experimental procedures and techniques.

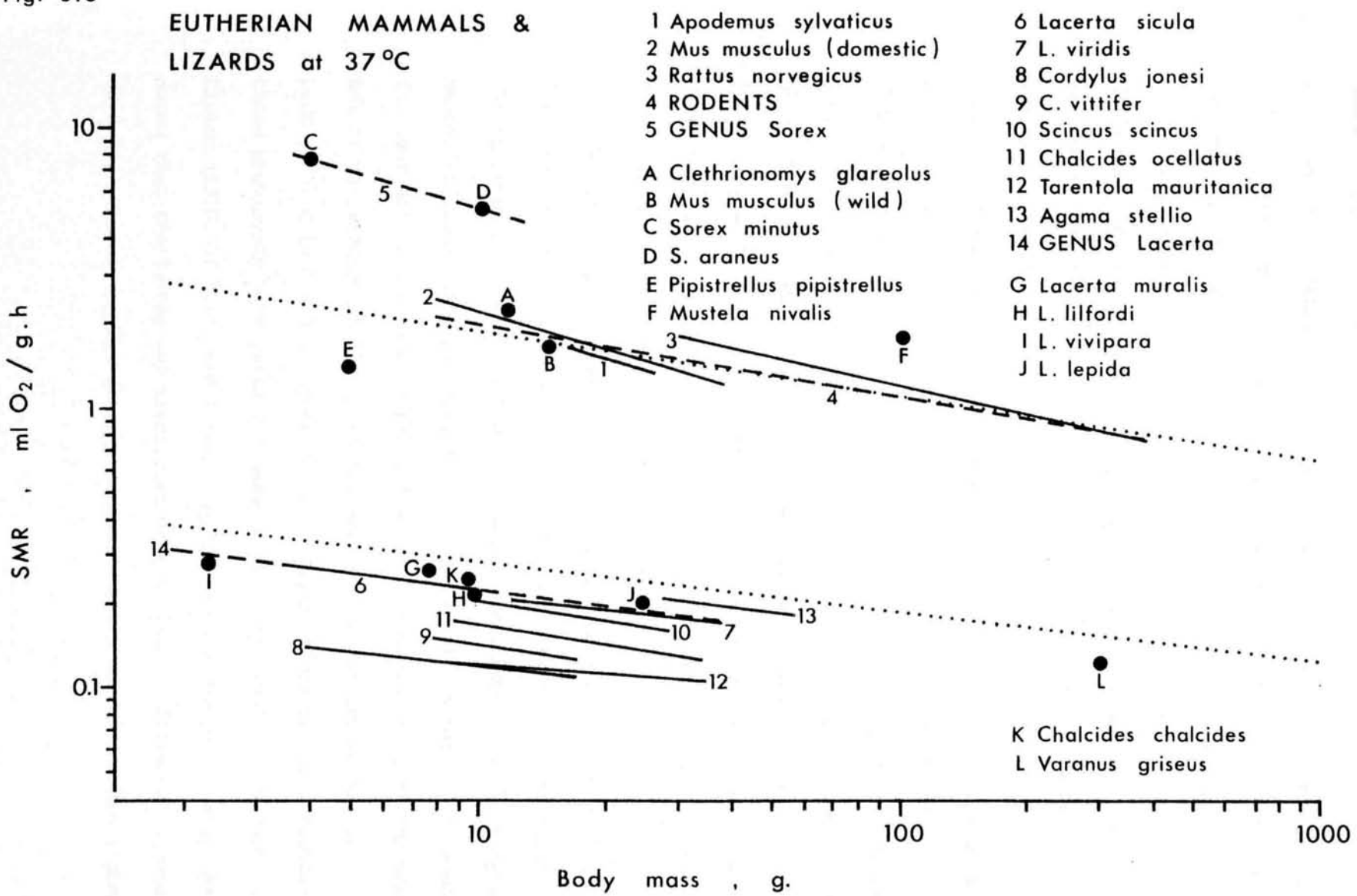
Benedict (1932) compared the metabolic rates of men with those of very large reptiles, although not lizards, extrapolated 37°C and calculated the heat production of giant tortoises, alligators and pythons were lower by factors of approximately 3, 3.5 and 5 respectively. Dawson & Bartholomew (1956) found that earlier measurements of hummingbirds (Morrison, Ryser and Dawe, 1953) and shrews (Pearson, 1950) were between 8.8 and 11.5 times higher than those they obtained at 37°C from the small lizards *Sceloporus occidentalis* and *Uta stansburiana*, weighing between 2 and 4 g. In a study of the larger lizard *Dipsosaurus dorsalis* weighing 69 g, Dawson & Bartholomew (1958) reported oxygen consumption rates lower than those previously measured from the similarly sized rodents *Dipodomys panamintinus* and *Citellus leucurus* (Dawson, 1955) by factors of 6.7 and 7.2, respectively. Bartholomew & Tucker (1963) compared the resting metabolism of the large Australian agamid lizard *Amphibolorus barbatus*, weighing 373 g with that of a 430 g guinea pig (Brody, 1945) and found that of the latter was 5.6 times greater. A similar, approximately 6-fold, difference was also reported by Bennett (1972a) between 674 g *Varanus gouldi* and a hypothetical mammal of equal body mass predicted by the equation of Kleiber (1961). Else & Hulbert (1981)

determined the resting oxygen consumption rates of both *Mus musculus*, 32.1 g, and the agamid lizard *Amphibolorus nuchalis*, 34.3 g, reporting a value 8.1 times greater in the mammal. This latter value is of particular interest, since it relates to determinations of reptilian and mammalian metabolism produced using the same techniques.

Although from the present study it is clear that all eutherian mammals have rates of resting oxygen consumption considerably higher than those of the reptiles examined, it is not possible to quantify the difference by a single factor for two reasons. First, it has been established that both the reptiles and mammals are metabolically heterogeneous groups, and therefore the extent of the difference will depend upon which representatives of each are compared (Fig. 3.6). For example, considering animals weighing less than about 15 g, the chiropteran *Pipistrellus pipistrellus* possess a resting metabolic level only 5.4 times greater than that of the anguid lizard *Anguis fragilis*, extrapolated to 37°C, whereas shrews display levels of oxygen consumption 55.5 times higher than lizards of the genus *Cordylus*. The range would be even greater if representatives of the monotremes and marsupials, two mammalian orders with relatively low metabolic levels not examined in the present study, were included in the comparisons. However, if typical examples of lizards and eutherian mammals are compared, such as lacertids and rodents, a 25 g mammal will have a resting metabolic rate approximately 7.5 times that of a similarly sized reptile. Also, it should be noted that these values refer to reptiles acclimated to 30°C. If they had been acclimated to 37°C, approximately the same body temperature as the mammals, any metabolic compensation to this higher temperature would have reduced their SMLs and therefore the extent of the differences

Figure 3.6 Summary diagram of the relationships between standard metabolic rate (SMR) in mammals under conditions of thermoneutrality, and lizards at 37°C, and body mass. Regression lines (see Tables 2.4, 2.5 and 3.1) extend across the body mass range over which they were determined. Points are plotted at the mean SMRs and body mass of species from which less extensive data were obtained (see Tables 2.3 and 3.2). The upper and lower dotted lines are those produced by Kleiber (1961), BMR = 3.417. $Mass^{0.75}$, for eutherian mammals and Bennett & Dawson (1976), SMR = 0.424.$Mass^{0.82}$, for lizards at 37°C, respectively.

Fig. 3.6


EUTHERIAN MAMMALS &
LIZARDS at 37 °C
1 Apodemus sylvaticus
2 Mus musculus (domestic)
3 Rattus norvegicus
4 RODENTS
5 GENUS Sorex
A Clethrionomys glareolus
B Mus musculus (wild)
C Sorex minutus
D S. araneus
E Pipistrellus pipistrellus
F Mustela nivalis
6 Lacerta sicula
7 L. viridis
8 Cordylus jonesi
9 C. vittifer
10 Scincus scincus
11 Chalcides ocellatus
12 Tarentola mauritanica
13 Agama stellio
14 GENUS Lacerta
G Lacerta muralis
H L. lilfordi
I L. vivipara
J L. lepida
K Chalcides chalcides
L Varanus griseus
SMR , ml O2 / g.h
10
1
0.1
10
100
1000
Body mass , g.

between them and the mammals would have been slightly greater (see Chapter 5).

The second reason is that, as already discussed (Chapters 2.3.2 & 2.3.3), the exponents relating metabolism to body mass in reptiles and mammals are different. Therefore, not only are the metabolic rates of these two groups size dependent, so is the extent of the difference between them. As the general exponent of mammals appears to be lower than that of reptiles the difference in resting oxygen consumption will be greater between small species than larger ones This convergence at higher body masses explains much of the variation in the results of the earlier comparative studies described above. The greatest differences, of 8.8 to 11.5 times, were reported between very small lizards and higher vertebrates (Dawson & Bartholomew, 1956), while those for very large reptiles and mammals (Benedict, 1932) were less than 5-fold. Data from medium sized species produced intermediate factors of 5.5-8.1 (Dawson & Bartholomew, 1958; Bartholomew & Tucker, 1963; Bennett, 1972a, Else & Hulbert, 1981).

Taking the general exponents of mammals and reptiles as 0.75 and 0.85, respectively, it is possible to produce an equation describing the difference between the BMRs of rodents, which appear to be a typical mammalian group, and the upper limit of the metabolic band of lizards. The mean BML of the data obtained from adult rodents is 3.197 and the SML of the lizards at the upper boundary of the saurian metabolic band at 37°C is 0.419 (Chapter 2.3.4). These values are very similar to those previously calculated for mammals (Kleiber, 1961) and Bennett & Dawson (1976) of 3.417 and 0.424, respectively, although it should be noted that the latter was associated with a slightly different exponent of 0.82. Therefore, the resting metabolic rates of rodents are higher

than those of similarly sized lizards at 37°C by a factor given by the equation:

$$\frac{\text{BML mammal}}{\text{SML reptile @ 37°C}} = \frac{3.197\ \text{Mass (g)}^{0.75}}{0.419\ \text{Mass (g)}^{0.85}} = 7.630\ \text{Mass (g)}^{-0.10}$$

If comparisons are made between rodents and lizards of the genus *Lacerta*, a more metabolically typical group which are close to the centre of the saurian metabolic band, then the ratio is given by the equation:

$$\frac{3.197\ \text{Mass (g)}^{0.75}}{0.315\ \text{Mass (g)}^{0.85}} = 10.149\ \text{Mass (g)}^{-0.10}$$

Using the first of these two equations, the difference between the metabolic rates of mammals and reptiles weighing 1 g and 1 kg are factors of 7.6 and 3.8, respectively. These are comparable with values of 8.1 and 5.0 obtained by Bennett & Dawson (1976) for animals of these sizes. If comparisons are made between larger reptiles and mammals the differences are even less. For example, at 100 kg, a mass attained by the largest living lizard *Varanus komodoensis* and many crocodilians the difference would only be a factor of 2.4.

This convergence of the metabolic rates of reptiles and higher vertebrates at higher body masses has interesting implications for the energetics of extinct forms such as the dinosaurs (Chapter 1.2). Many of these animals are estimated to have weighed around 5 tonnes and the largest sauropods may have reached 100 tonnes. At these body masses the predicted differences between reptilian and mammalian resting metabolic rates would be factors of only 1.6 and 1.2, respectively. Therefore, at

a body temperature of 37°C the SMRs of dinosaurs may have been similar regardless of whether they possessed bradymetabolic and tachymetabolic physiology. However, it should be noted that these speculations are based on extrapolations of the regression equations to many orders of magnitude beyond the body mass range over which they were determined.

CHAPTER 4

THE OXYGEN CONSUMPTION RATES OF ISOLATED REPTILIAN AND MAMMALIAN TISSUES

4.1 INTRODUCTION

In Chapters 2 and 3 the extent of the differences between the BMLs of mammals and the SMLs of reptiles at a similar body temperature were established. The next objective of this study was to determine whether these reflect fundamental differences in the cellular metabolism of the two groups. This was investigated by measuring the metabolic rates of a range of isolated mammalian and reptilian tissues. Although a considerable amount of *in vitro* work has been conducted on mammals, very few measurements of the oxygen consumption rates of reptilian tissues have been made. The only study in which mammalian and reptilian tissues were compared under standard conditions (Hulbert & Else, 1981) examined only three types of tissues from a single representative of each taxa.

It has already been found that the metabolic rates of living animals are allometrically related to their body mass, the general exponents of these relationships being different in the mammals and reptiles (Chapters 2.3.2 & 3.3.2). Since similar trends could also exist at the cellular level it was considered necessary to compare tissues from representatives of the two groups covering a range of body sizes. The four tissues selected for these *in vitro* comparisons were liver, kidney cortex, cardiac and skeletal muscle. The principal animals used were rodents (*Mus musculus*, *Rattus norvegicus* and *Mesocricetus auratus*) and lizards of the genus *Lacerta* (*L. sicula*, *L. vivipara* and *L. viridis*), from both of which extensive data on

the relationships between oxygen consumption and body mass had already been collected under appropriate conditions from living animals. As it had been established that both the mammals and reptiles encompass a range of metabolic levels (Chapters 2.3.3 & 3.3.3) it was decided to also examine tissues from some additional species to investigate whether this heterogeneity reflects differences in tissue metabolism. However, since measuring the oxygen consumption rates of tissues required sacrificing the animals, the numbers of individuals and species (*Pipistrellus pipistrellus*, *Cordylus jonesi*, *Chalcides ocellatus* and *Agama stellio*) used were much less than in the studies of the metabolic rates of living animals.

To extend the range of tissues from which data were obtained, a total of eight types were compared in a single mammal and reptile species. In addition to the four tissues listed above brain, lung, stomach and intestinal smooth muscle were examined in the laboratory mouse *Mus musculus* and *Cordylus jonesi*, a cordylid lizard of similar body mass.

4.2 MATERIALS AND METHODS

4.2.1 Animals

Both mammals and reptiles were housed and maintained under conditions identical to those described in Chapters 2.2.1 & 3.2.1. The reptiles used in this study were the same individuals which had previously been used to determine the oxygen rates of living animals.

4.2.2 Determination of the oxygen consumption rates of isolated tissues

The *in vitro* metabolic rates of tissues were measured using a YSI Biological Oxygen Monitor, Model 53 (Yellow Springs Instrument Company). This instrument utilises the principle of the Clark polarographic electrode to measure dissolved oxygen pressure in aqueous solutions. A polarising voltage is applied between two electrodes bathed in a potassium chloride solution electrolyte, which is separated from the reaction medium by a teflon membrane. Oxygen dissolves into the electrolyte from the medium containing the tissue sample and reacts at the cathode, causing a current to flow through the cell. Since this oxygen is rapidly consumed at the cathode its concentration in the electrolyte is extremely low, and therefore the rate at which it diffuses across the membane is directly proportional to the absolute pressure of oxygen in the external medium. Consequently, the oxygen concentrations of solutions in contact with the membrane can be followed by monitoring the magnitude of the current flowing between the two electrodes. After calibration the instrument produced a linear output signal of 0-10 mV, which was displayed on a potentiometric recorder corresponding to relative oxygen levels between 0 and 100% saturated. The rate of decline of the oxygen concentration in the medium described

by the trace was converted into an actual amount of oxygen consumed from the solubility of this gas in Ringer's solution at the temperature and partial pressure used of 0.020 ml O_2 (STP)/ml (Davison, 1970).

During experiments samples of tissues were suspended in a medium containing (in mM): Na^+, 125; K^+, 5; Mg^{++}, 1; Ca^{++}, 1; Cl^-, 129; buffered with 10 mM Hepes at pH 7.4. 10 mM glucose and 5 mM sodium pyruvate was provided as substrate, concentrations which preliminary experiments had shown were not rate limiting under the conditions used. All chemicals used were supplied by BDH Chemicals Ltd. and Sigma Chemical Company Ltd. The volume of medium used in the measurement chambers was normally 5 ml, although this was occasionally reduced to 2.5 ml when only small amounts of tissue could be obtained. The medium was agitated with a circular magnetic stirrer, shaped to produce adequate movement of the fluid over the electrode membrane without breaking up the tissue slices.

4.2.3 Experimental procedures

To ensure the *in vitro* measurements were comparable to those obtained from living animals, all tissues were taken from post-absorptive mammals which had been maintained within their thermoneutral zone for 24 hours immediately prior to being killed. Reptiles were kept for a similar period at 37°C, the temperature at which all subsequent tissue oxygen consumption rates were determined.

Mammals were killed by cervical dislocation and reptiles by decapitation. The appropriate tissues were removed and immediately transferred to an oxygenated medium of the same composition as that used in the measurement chambers. All subsequent preparative procedures were conducted on cracked ice using pre-cooled instruments.

Tissues were used in the form of thin slices, except skeletal muscle which was teased apart into loosely associated bundles of fibres. The skeletal muscle used was taken from the hind limbs of the animals. Slices were prepared using a perspex Stadie-Riggs hand microtome. The blade was drawn carefully through the tissue with a steady pressure, avoiding any excessive shearing action which would rupture the cells. The slices were then trimmed to a maximum size of 5 mm square with a scapel blade. To minimise deterioration the tissues were kept in chilled oxygenated medium at approximately 5°C until introduction to the chambers. To avoid excessive storage times the oxygen consumption rates of a maximum of four different tissues were measured from any individual animal. These were always determined in the same sequence of either liver, kidney cortex, cardiac muscle and skeletal muscle, or alternatively brain, large intestine, stomach and lung. This ensured that the storage times of all samples of the same type of tissue were similar, and therefore the data obtained from them are comparable. No tissues were normally stored for more than 30 minutes before use.

Before each tissue was placed in the chamber the slices were removed from the storage medium, gently blotted between filter paper to remove excess fluid, and weighed. Wet weights of tissues were used in calculations rather than dry weights to allow direct comparison of oxygen consumption rates with those of living animals. Before each determination the medium in the chamber was saturated with a mixture of 95% oxygen and 5% carbon dioxide. The tissue sample was placed in the medium and after a five minute equilibration period, during which oxygenation continued, the electrode was fitted into the chamber. Oxygen now consumed by the tissue was not replaced, resulting in a fall in dissolved oxygen concentration. This uptake by each tissue sample

was recorded for between two and five minutes. For each set of determinations a blank was also run, consisting of the appropriate volume of medium without any tissue, to determine any residual fall in oxygen levels due to consumption by the electrode and leakage from the chamber.

4.3 RESULTS AND DISCUSSION

4.3.1 Determinations of *in vitro* tissue metabolic rates

The oxygen consumption rates of isolated liver, kidney cortex, cardiac and hind limb skeletal muscle from six species of lizard and four mammals are presented in Table 4.1 and Figs. 4.1 to 4.4. Insufficient cardiac muscle could be obtained from *Lacerta vivipara*, and hind limb skeletal muscle from this species and *Pipistrellus pipistrellus* to enable the oxygen consumption rates of these tissues to be determined. Too much importance should not be attached to the absolute metabolic rates of individual tissues, or the differences between them, since the storage times of tissues varied. However, all samples of the same tissue type were stored for a similar period, and therefore the data obtained from them are comparable. Measurements of rodent tissues are similar to those previously reported (Martin & Fuhrman, 1955; Ismail-Beigi & Edelman, 1971). However, the oxygen consumption rates of reptilian liver are somewhat higher than those obtained by Wong, Chiu & Wong (1975) from the gekkonid *Hemidactylus bowringii* (0.235 ml O_2/g wet wt.h at 35°C) and Hulbert & Else (1981) from the agamid *Amphibolurus nuchalis* (0.90 ml O_2/g dry wt.h at 37°C). A potential reason for the lower values in the previous studies could be that they were determined manometrically, with measurement periods extending over 2 hours after the death of the animal. In the present study measurements of isolated liver metabolism were normally completed within 15 minutes. Also, it should be noted that media composition and substrates used, factors known to influence *in vitro* determinations of tissue metabolism (Krebs, 1950), varied between studies.

Sufficient data were obtained from the lizard *Lacerta viridis* and the rodents *Mus musculus*, *Rattus norvegicus* and *Mesocricetus auratus* to

Table 4.1 The *in vitro* oxygen consumption rates of isolated mammalian and reptilian tissues

Species	Liver			Kidney cortex		
	n	Body mass, g mean	O_2 consumption, ml/g.h (mean ± S.E.)	n	Body mass, g mean	O_2 consumption, ml/g.h (mean ± S.E.)
Reptiles						
Lacerta sicula	3	6.2	1.019 (± 0.021)	3	6.2	1.664 (± 0.093)
Lacerta vivipara	8	3.3	1.045 (± 0.046)	6	3.2	1.875 (± 0.111)
Lacerta viridis	18	20.4	0.790 (± 0.015)	16	20.5	1.612 (± 0.048)
Cordylus jonesi	15	11.9	0.670 (± 0.017)	15	11.9	1.451 (± 0.047)
Chalcides ocellatus	3	15.3	0.857 (± 0.034)	3	15.3	1.662 (± 0.023)
Agama stellio	2	29.5	1.022 (± 0.018)	2	29.5	1.126 (± 0.026)
Mammals						
Pipistrellus pipistrellus	5	4.6	2.381 (± 0.087)	5	4.6	4.781 (± 0.132)
Mus musculus	58	16.8	2.917 (± 0.026)	17	19.3	3.909 (± 0.072)
Rattus norvegicus	18	78.5	2.437 (± 0.051)	9	73.3	3.936 (± 0.078)
Mesocricetus auratus	26	79.9	2.393 (± 0.041)	14	83.7	4.017 (± 0.098)

Table 4.1 Continued

Species	Cardiac muscle			Skeletal muscle		
	n	Body mass, g mean	O_2 consumption, ml/g.h (mean ± S.E.)	n	Body mass, g mean	O_2 consumption, ml/g.h (mean ± S.E.)
Reptiles						
Lacerta sicula	3	6.2	2.869 (± 0.071)	3	6.2	0.252 (± 0.008)
Lacerta viridis	14	19.8	1.683 (± 0.067)	8	18.4	0.216 (± 0.009)
Cordylus jonesi	15	11.9	2.423 (± 0.083)	15	11.9	0.256 (± 0.009)
Chalcides ocellatus	3	15.3	2.456 (± 0.120)	3	15.3	0.254 (± 0.016)
Agama stellio	2	29.5	2.165 (± 0.075)	2	29.5	0.207 (± 0.011)
Mammals						
Pipistrellus pipistrellus	4	4.6	4.003 (± 0.164)			
Mus musculus	17	19.3	2.883 (± 0.044)	16	18.7	0.585 (± 0.017)
Rattus norvegicus	9	73.3	2.802 (± 0.072)	9	73.3	0.509 (± 0.018)
Mesocricetus auratus	16	80.7	2.965 (± 0.063)	15	83.7	0.595 (± 0.029)

Table 4.2 Regression parameters of the relationship between *in vitro* oxygen consumption rate and body mass for isolated reptilian and mammalian tissues at 37°C

Tissue	Species	n	Body mass, g range (mean)	Intercept, a	Exponent, b, ± 95% confidence limits	r
LIVER	Lacerta viridis	18	10.5-38.2 (20.4)	0.975	-0.07 ± 0.12	-0.31
	GENUS LACERTA	29	2.8-38.2 (14.2)	1.267	-0.15 ± 0.05*	-0.76
	Mus musculus	58	5.9-39.3 (16.8)	3.244	-0.04 ± 0.04	-0.24
	Mesocricetus auratus	26	32.5-137 (79.9)	3.572	-0.09 ± 0.06*	-0.58
	Rattus norvegicus	18	35.7-154 (78.5)	3.860	-0.11 ± 0.08*	-0.57
	RODENTS	102	5.9-154 (43.8)	3.905	-0.11 ± 0.002*	-0.82
KIDNEY CORTEX	Lacerta viridis	16	12.2-33.4 (20.5)	2.114	-0.09 ± 0.22	-0.23
	GENUS LACERTA	25	2.8-33.4 (14.6)	1.988	-0.07 ± 0.06*	-0.46
	Mus musculus	17	9.2-39.3 (19.3)	4.008	-0.01 ± 0.09	-0.05
	Mesocricetus auratus	14	32.5-137 (75.0)	5.243	-0.06 ± 0.10	-0.39
	Rattus norvegicus	9	43.3-136 (73.2)	2.719	0.09 ± 0.09	0.64
	RODENTS	40	9.2-137 (50.9)	3.911	0.00 ± 0.03	0.02

*$p < 0.05$

Table 4.2 continued

Tissue	Species	n	Body mass, g range (mean)	Intercept, a	Exponent, b, ± 95% confidence limits	r
CARDIAC MUSCLE	Lacerta viridis	14	10.5-33.4 (19.8)	2.960	-0.04 ± 0.17	-0.13
	GENUS LACERTA	17	5.1-33.4 (17.4)	3.104	-0.05 ± 0.09	-0.31
	Mus musculus	17	9.2-39.3 (19.3)	3.193	-0.04 ± 0.07	-0.26
	Mesocricetus auratus	16	32.5-137 (80.7)	2.580	0.03 ± 0.09	0.21
	Rattus norvegicus	9	43.3-136 (73.3)	2.131	0.06 ± 0.15	0.36
	RODENTS	42	9.2-137 (54.2)	2.801	-0.01 ± 0.03	0.09
SKELETAL MUSCLE	Lacerta viridis	8	12.4-26.0 (18.4)	0.415	-0.23 ± 0.42	-0.48
	GENUS LACERTA	11	5.1-26.0 (15.0)	0.339	-0.16 ± 0.12*	-0.71
	Mus musculus	16	9.2-39.2 (18.7)	0.618	-0.03 ± 0.12	-0.13
	Mesocricetus auratus	15	32.5-137 (83.7)	1.074	-0.14 ± 0.18	-0.43
	Rattus norvegicus	9	43.3-136 (73.3)	1.069	-0.18 ± 0.16*	-0.70
	RODENTS	40	9.2-137 (55.9)	0.661	-0.04 ± 0.05	-0.26

*$p < 0.05$

Figures 4.1-4.4 Relationships between the oxygen consumption rates of isolated reptilian and mammalian tissues and body mass at a measurement temperature of 37°C. Solid and broken lines were fitted by linear regression analysis to measurements of all tissues from rodents and lizards of the genus *Lacerta*, respectively (see Table 4.2). For key see Fig. 4.1.

Figure 4.1 Liver

Figure 4.2 Kidney cortex

Figure 4.3 Cardiac muscle

Figure 4.4 Skeletal muscle.

Fig. 4.1

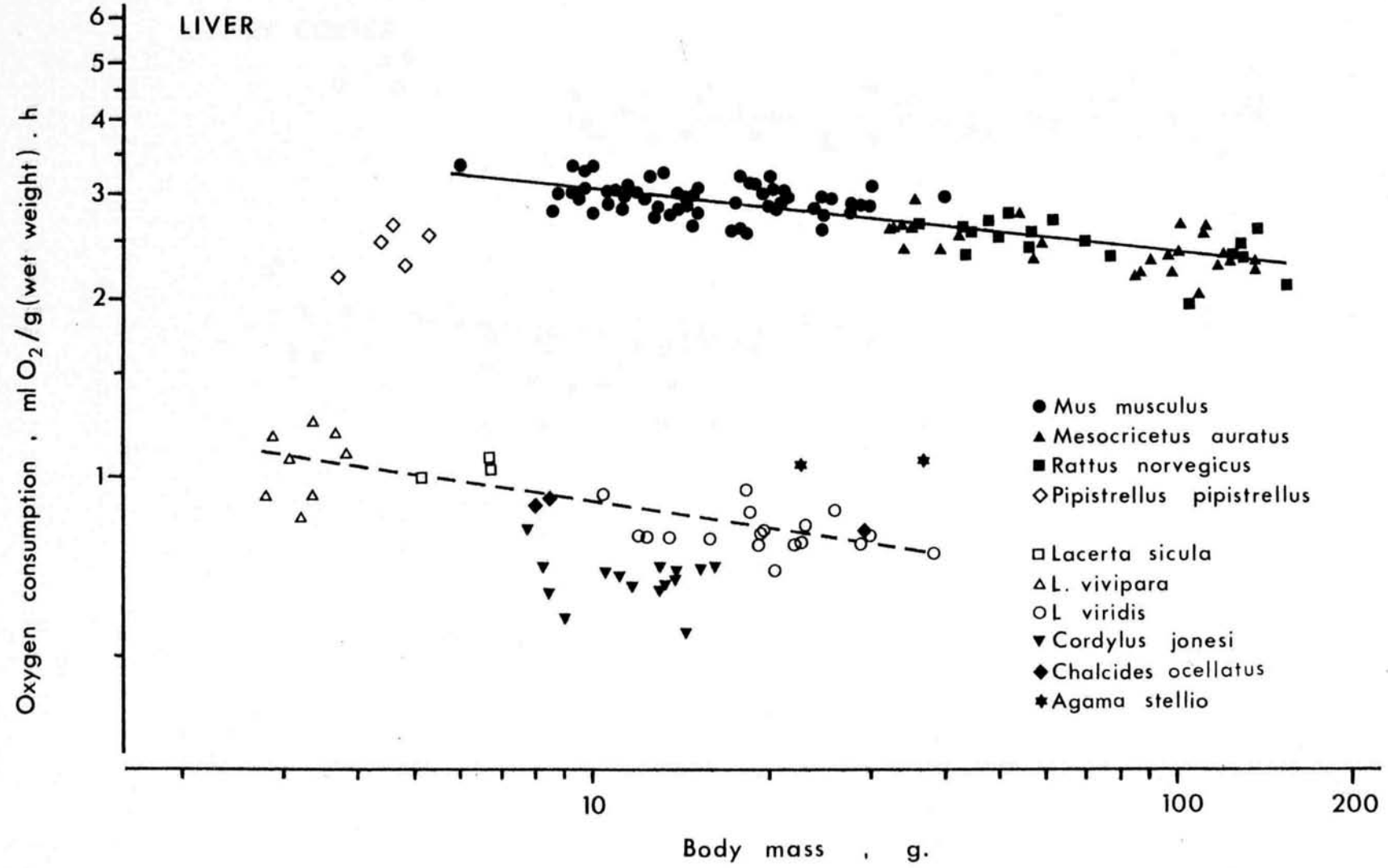

LIVER
Oxygen consumption . ml O_2/g (wet weight) . h
6
5
4
3
2
1
10
100
200
Body mass . g.
● Mus musculus
▲ Mesocricetus auratus
■ Rattus norvegicus
◇ Pipistrellus pipistrellus
□ Lacerta sicula
△ L. vivipara
○ L viridis
▼ Cordylus jonesi
◆ Chalcides ocellatus
✱ Agama stellio

Fig. 4.2

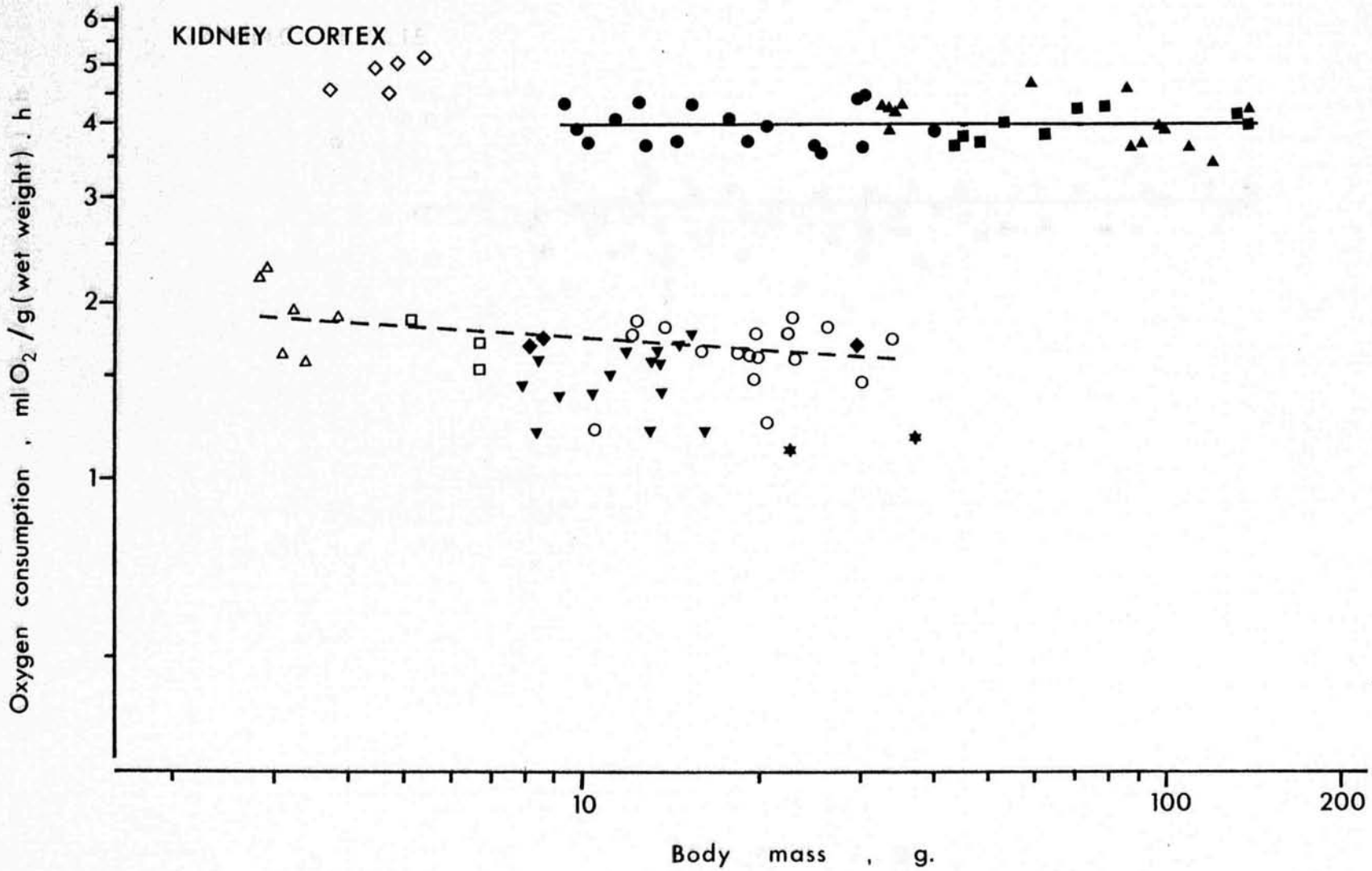

KIDNEY CORTEX
Oxygen consumption , ml O_2 /g (wet weight) . h
6
5
4
3
2
1
10
100
200
Body mass , g.

Fig. 4.3

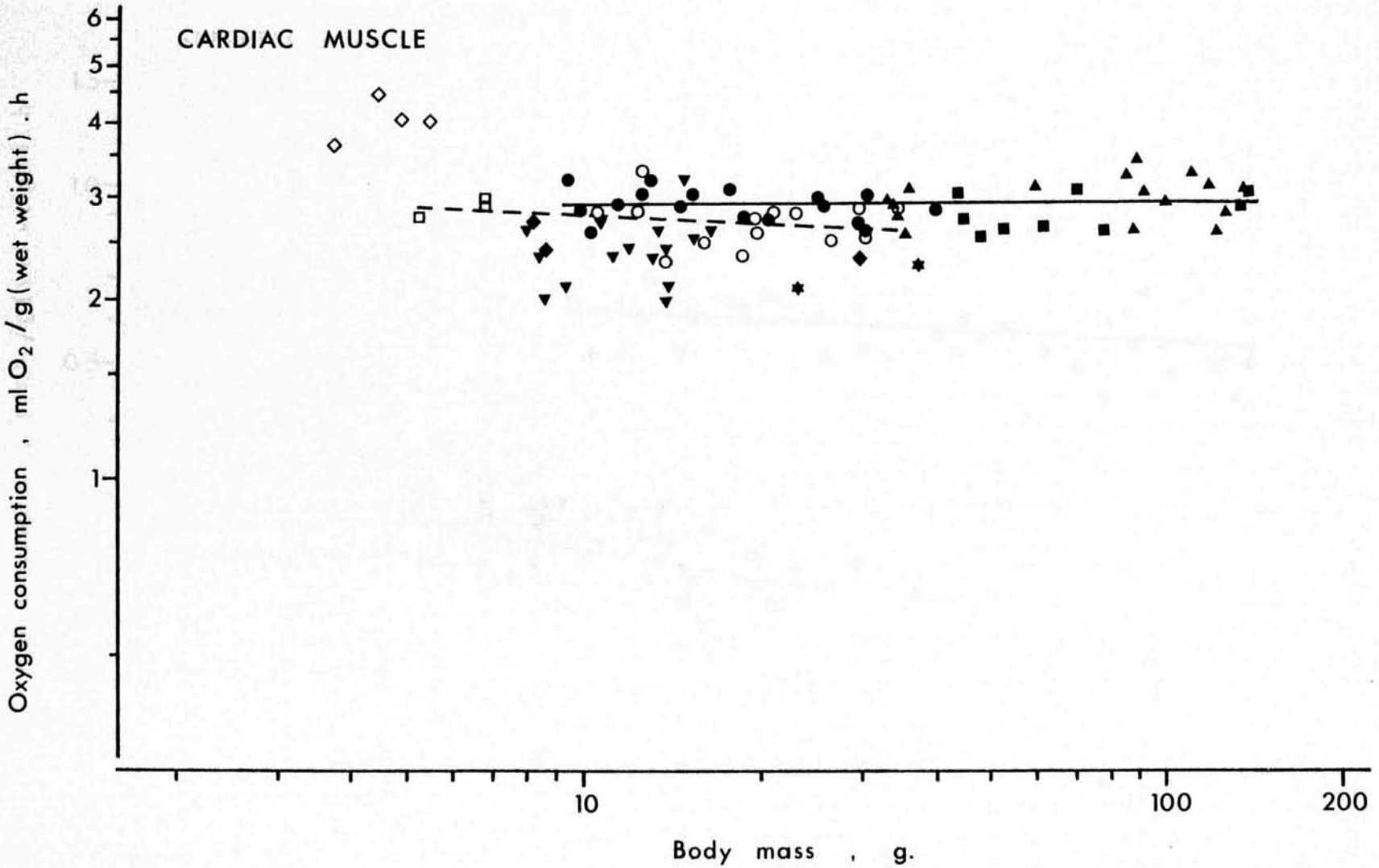
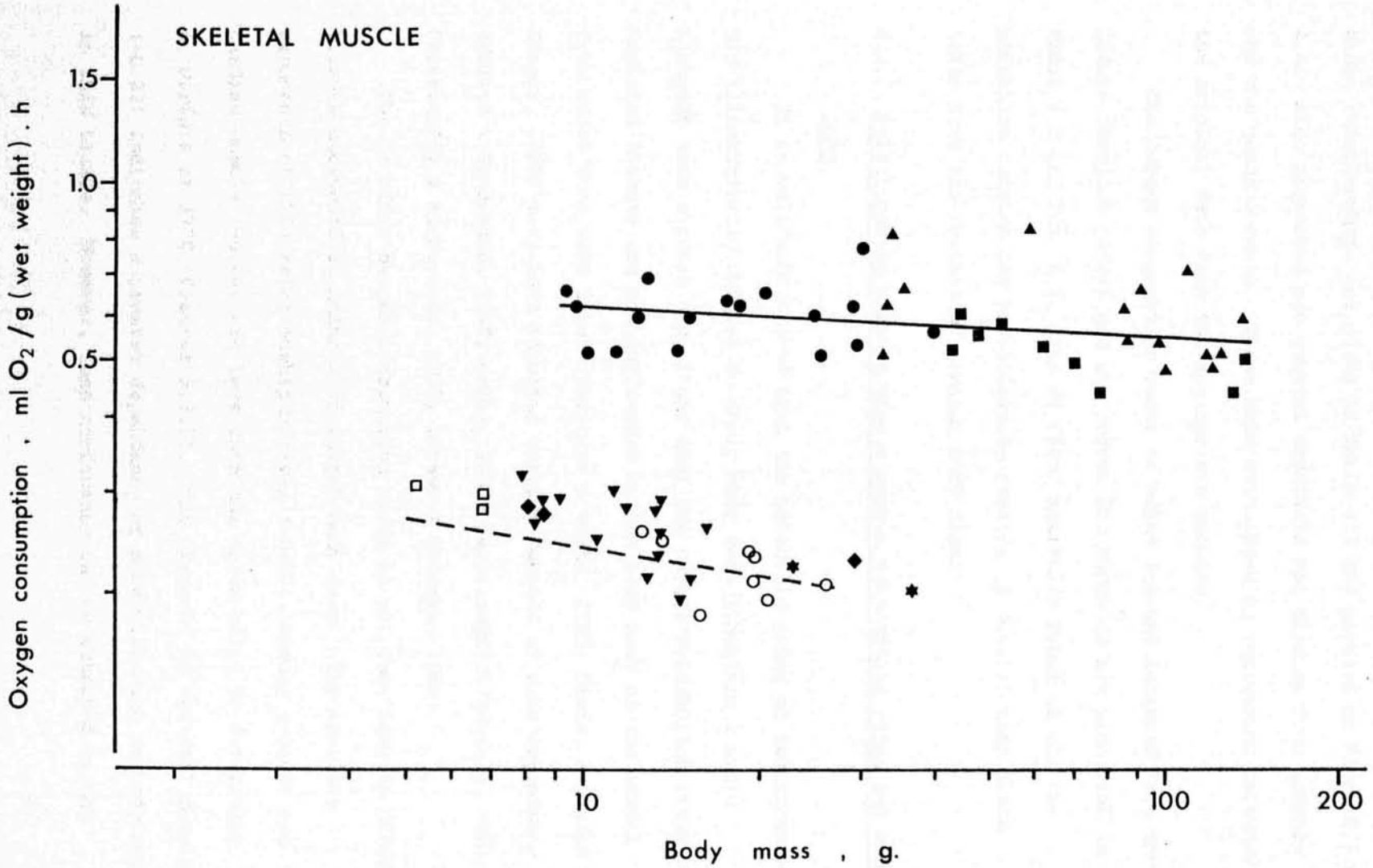

CARDIAC MUSCLE
Oxygen consumption , ml O_2 / g (wet weight) . h
6
5
4
3
2
1
10
100
200
Body mass , g.

Fig. 4.4


SKELETAL MUSCLE
Oxygen consumption , ml O_2 / g (wet weight) . h
1.5
1.0
0.5
10
100
200
Body mass , g.

examine the influence within species of body mass on the *in vitro* metabolic rates of these four tissues. The regression parameters of these relationships are given in Table 4.2 and plotted on Figs. 4.1 to 4.4. Also presented are general equations for tissues from rodents and the genus *Lacerta*. These were calculated by regressing together the original data from the appropriate species.

The oxygen consumption rates of eight tissues isolated from the lizard *Cordylus jonesi* and the rodent *Mus musculus* are presented in Table 4.3 amd Fig. 4.5. The *in vitro* metabolic rates of all the mammalian tissues are significantly greater ($p < 0.01$) than those taken from the reptile of similar body mass.

4.3.2 Relationships between tissue oxygen consumption rates and body mass

It is well established that the metabolic rates of vertebrates are allometrically related to their body mass (Chapters 2 & 3). Although some studies have found that the oxygen consumption rates of isolated tissues are not influenced by the body mass of the animal from which they were taken (Terroine & Roche, 1925; Grafe, Reinwein & Singer, 1925) most have reported varying degrees of size dependency (Elliot & Henderson, 1948; Krebs, 1950; Bertalanffy & Eastwick, 1953; Bertalanffy & Pirozynski, 1953; Oikawa & Itazawa, 1984).

The *in vitro* oxygen consumption rates of all four *Lacerta viridis* tissues decreased in animals of larger body mass. The absolute exponents of this relationship in liver (-0.07), kidney (-0.09) and cardiac muscle (-0.04) are less than the value of -0.15 for living *L. viridis* at 37°C (Chapter 2.3.2). The exponent of skeletal muscle (-0.23) indicates a greater dependency of metabolic rate on body mass in this tissue. However, less confidence can be attached to the

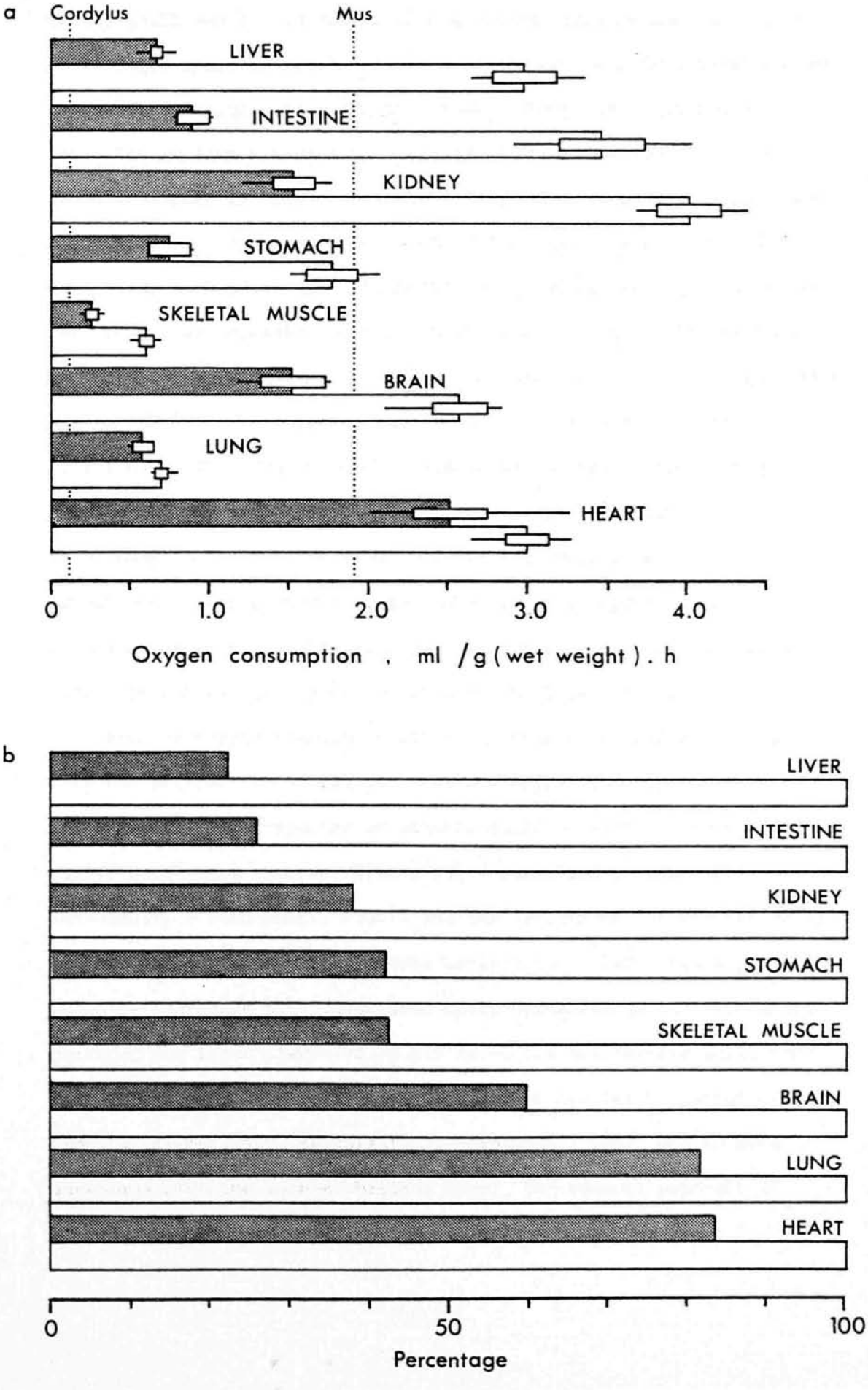
Table 4.3 *In vitro* oxygen consumption rates at 37°C of tissues isolated from the lizard *Cordylus jonesi* (mean body mass 13.4 g) and the rodent *Mus musculus* (14.3 g).

Tissue	Oxygen consumption ml/g.h mean ± SE		Comparison (t-test)	Mammal / Reptile
	Cordylus jonesi	Mus musculus		
Liver	0.653 ± 0.017	2.916 ± 0.099	<0.001	4.47
Kidney cortex	1.492 ± 0.064	3.931 ± 0.091	<0.001	2.63
Cardiac muscle	2.454 ± 0.111	2.931 ± 0.063	<0.01	1.19
Skeletal muscle	0.246 ± 0.012	0.579 ± 0.020	<0.001	2.35
Brain	1.495 ± 0.105	2.510 ± 0.080	<0.001	1.68
Intestine	0.867 ± 0.049	3.391 ± 0.127	<0.001	3.91
Stomach	0.721 ± 0.060	1.714 ± 0.079	<0.001	2.38
Lung	0.555 ± 0.034	0.680 ± 0.018	<0.01	1.23

Figure 4.5 (a) The mean oxygen consumption rates of eight tissues isolated from the reptile *Cordylus jonesi* (mean body mass 13.4 g) and the mammal *Mus musculus* (14.3 g). Rectangles represent ± 2 S.E. and bars the range. The SMRs calculated for living *Cordylus jonesi* and *Mus musculus* with these body masses, 0.12 and 1.91 ml O_2/g.h, respectively, are shown by the broken lines (see Chapter 2.3).

(b) The reptilian values expressed as a percentage of the corresponding tissue from the mammal.

Fig. 4.5


a
Cordylus
Mus
LIVER
INTESTINE
KIDNEY
STOMACH
SKELETAL MUSCLE
BRAIN
LUNG
HEART
0
1.0
2.0
3.0
4.0
Oxygen consumption , ml / g (wet weight) . h
b
LIVER
INTESTINE
KIDNEY
STOMACH
SKELETAL MUSCLE
BRAIN
LUNG
HEART
0
50
100
Percentage

accuracy of this exponent, since the number of measurements was relatively small and in comparison with the other tissues the metabolism of isolated skeletal muscle was low, making accurate determinations of oxygen consumption rates more difficult. There are no previous reptilian studies with which these exponents can be compared, although the allometries of tissue metabolism in another lower vertebrate, the carp *Cyprinus carpio*, have been examined by Oikawa & Itazawa (1984). This study also found that the metabolic rates of isolated tissues were less body mass dependent than those of living animals. The exponents reported for hepatopancreas (-0.0741) and kidney (-0.0575) in this fish are very similar to those obtained from homologous tissues of *L. viridis*. The intra-generic exponents for *Lacerta* kidney (-0.07), cardiac (-0.05) and skeletal muscle (-0.16) are very similar to those calculated for *L. viridis* alone, however, it should be noted that the majority of the measurements were made from this species. The exponent for liver (-0.15) is closer to the mass specific metabolic rate exponent for this genus at 37°C of -0.20 (Chapter 2.3.2).

Similar trends are also evident in isolated mammalian tissues. Although Kleiber (1941) claimed that the oxygen consumption rates of liver tissue from 5 species of mammals declined with an exponent of -0.24, subsequent workers (Krebs, 1950; Bertalauffy & Eastwick, 1953; Bertalauffy & Pirozynski, 1953), and the results of the present study, support the contention that tissue metabolism is less strongly influenced by body mass than organismal basal metabolic rate. Exponents produced for liver tissue of -0.018 to -0.116 intraspecifically for rats (Bertalanffy & Pirozynski, 1953) and -0.115 for 9 species of mammals (Krebs, 1950; Bertalanffy & Pirozynski, 1953) are in good agreement with the values obtained here. The general exponent of

-0.064 for kidney cortex (Krebs, 1950; Bertalanffy & Pirozynski, 1953) is similar to that produced intra-specifically for the hamster (-0.06) and mouse (-0.01), however, the metabolism of rat kidney increased in animals of larger body mass. Bertalanffy & Eastwick (1953) obtained an exponent of -0.065 from rat skeletal muscle, which is less than the absolute value produced here for this species (-0.18), but close to the composite value claculated for rodents (-0.04). Although Bertalanffy & Pirozynski (1953) produced an exponent of -0.05 for cardiac muscle of the rat, in the present study it was found that for this species, the hamster and rodents overall, its oxygen consumption was slightly higher in mammals of greater body mass. However, it should be noted that for none of the tissues in which metabolic rate increased in larger animals was the exponent significantly different from a value of zero ($p > 0.05$).

Therefore, in neither the reptiles nor mammals can the decrease in mass specific metabolic rates of larger animals be explained by a decline in tissue metabolism alone. One possible explanation of this discrepancy could be that an increasing proportion of the body is composed of tissues with lower respiration rates in larger animals (Kestner, 1934, 1936; Blank, 1934; Martin & Fuhrman, 1955), since it is known that the size of some metabolically active organs, including liver (Prothero, 1982), kidneys (Prothero, 1984), heart (Else & Hulbert, 1983) and brain (Martin, 1981), are allometrically related to body mass with exponents of less than unity. This idea is supported, in lower vertebrates at least, by the finding that the *in vitro* oxygen consumption of whole body preparations of carp decreased with an exponent of -0.153, a value almost identical with that obtained from living fish (Itazawa & Oikawa, 1983; Oikawa & Itazawa, 1984). Also, Krebs (1950)

suggested in mammals that under the control of the nervous system in the animal the oxygen consumption of skeletal muscle may change with body mass in a way more closely paralleling the differences in organismal BMR.

4.3.3 Differences in the *in vitro* metabolic rates of homologous reptilian and mammalian tissues

The oxygen consumption rates of all mammalian tissues examined in this study are higher than the equivalent tissues from reptiles, although the extent varies considerably. All differences in tissue metabolism are less than at the organismal level, at which the basal oxygen consumption rate of a living mouse weighing approximately 15 g is 11.69 and 16.48 times greater than those of similarly sized *Lacerta viridis* and *Cordylus jonesi* respectively, at 37°C (Chapter 2.3).

(i) Liver

Among lizards the pattern of variation in liver metabolism is similar to that of intact reptiles (Chapter 2.3.3), with the genera possessing the higher SMLs displaying the greatest *in vitro* oxygen consumption rates. However, the extent of these differences is less than those between living animals. For example, the SML of *Lacerta viridis* at 37°C is approximately 1.74 times higher than that of *Cordylus jonesi*, although the oxygen consumption of liver tissue is only about 1.18 times greater.

Liver from the three species of rodents had a similar metabolic rate, allowing for differences in body mass, but that of *Pipistrellus pipistrellus* was lower. However, the oxygen consumption of isolated chiropteran liver was 0.73 times that of a mouse extrapolated to a

similar body mass, although this mammal possessed a BML of only 0.59 times that of the rodent.

These variations with both reptiles and mammals mean that, as with living animals, no single value can be produced to describe the difference in liver respiration between the two groups. For example, the metabolic rate of mouse liver is 3.61 and 4.47 times higher than those of *Lacerta* and *Cordylus*, respectively. A similar factor was reported by Hulbert & Else (1981), who found that respiration, expressed per unit dry weight of tissue, of mouse liver was 5.10 times greater than that of the agamid lizard *Amphibolurus nuchalis*.

(ii) Kidney cortex

The oxygen consumption of kidney cortex is higher than liver in both reptiles and mammals. Its metabolism is 2.28 and 2.04 times greater in *C. jonesi* and *L. viridis*, factors which are comparable to a value of 2.26 fold difference between the respiration of kidney and hepatopancreas tissue in the carp (Oikawa & Itazawa, 1984). The increased metabolic rate of this tissue may be due to high Na^+-K^+-ATPase activity (Hulbert & Else, 1981) which is responsible for the transport of large quantities of monovalent cations across the tubule walls. This pumping will continue, and could even be stimulated, in the ionic conditions experienced *in vitro*.

The differences in respiration rate between taxa were less in this more specialised tissue than for liver. Mouse kidney had an oxygen consumption rate 2.63 times higher than *C. jonesi* of similar body mass, compared with a value of 4.91 reported by Hulbert & Else (1981) for the mouse and *Amphibolurus nuchalis*.

(iii) Muscle

(a) Skeletal

The *in vitro* metabolic rate of skeletal muscle was the lowest of any tissue examined in the present study. This was also found to be the situation in the carp by Oikawa & Itazawa (1984). However, of all these tissues the performance of isolated skeletal muscle probably bears the least resemblance to its oxygen consumption in the living animal. Normally most of the energy metabolism of muscle cells is related to the ATPase activity of the contractile proteins in the myofibrils. Contraction of these, to produce movement or muscle tonus, requires the structural integrity of the muscle and its efferent nerve supply. Therefore, the *in vitro* metabolism of this tissue is probably only a small fraction of its level in life, particularly for mammals in which sustained muscle tonus is necessary for the maintenance of posture.

The metabolic rate of isolated skeletal muscle was similar within both the lizards and rodents, with that of the mouse being approximately 2.35 times greater than similar sized *Cordylus jonesi*.

(b) Cardiac

The oxygen consumption of cardiac muscle is relatively high, with mammalian heart tissue having only a slightly greater metabolic rate than that from reptiles. This is probably because in both groups, regardless of any thermogenic considerations, there is a need for sustained high levels of aerobic respiration to generate ATP in this continually active muscle. However, Else & Hulbert (1983) reported that the metabolic capacity of cardiac muscle from mammals is approximated twice that of reptiles.

The metabolic rate of *Pipistrellus pipistrellus* cardiac muscle is 1.41 times that of small rodents even though the BML of this species is lower. This may be related to the additional demands placed on the cardiovascular system of these mammals by flight.

(c) Visceral Smooth (Intestine and Stomach)

These smooth muscles were found to have a much higher *in vitro* oxygen consumption than skeletal muscle. This is probably because, unlike skeletal muscle which requires nervous stimulation to initiate contraction, smooth muscle is myogenic and therefore some movement, and consequently ATP utilisation by the contractile elements, can continue in the isolated tissues.

In both smooth muscle samples examined the respiration of the mouse tissue was considerably higher than that of *Cordylus jonesi*, the differences being 3.91 and 2.38 times greater in the intestine and stomach, respectively.

(iv) Brain

The metabolic rate of brain tissue is relatively high, being 2.29 times greater than liver in *Cordylus jonesi* and 2.21 times that of hepatopancreas in the carp (Oikawa & Itazawa, 1984).

The respiration of mouse brain was only 1.68 times that of *C. jonesi*, a value similar to that of 2.21, obtained by Hulbert & Else (1981) from measurements of mouse and *Amphibolurus nuchalis* tissues. The small difference could be because in both mammals and reptiles energy turnover in this highly specialised tissue is principally determined by its functional requirements, such as ion transport, rather than any thermogenic factors.

(v) Lung

The metabolism of *Cordylus jonesi* lung tissue was only 0,85 times that of liver. Interestingly, although the respiratory structures of fish are anatomically very different, the respiration rate of gill filaments from the carp differed from hepatopancreas by a similar factor of 0.83 (Oikawa & Itazowa, 1984). The small 1.23 fold difference between mouse and *C. jonesi* lung appears to be primarily due to relatively low oxygen consumption by the mammalian tissue.

Therefore the variations in the resting metabolic rates of animals of different body masses and taxonomic groups are also present at the cellular level. However, although there is considerable variation between tissues, the extents of both these differences are less than those which exist between intact animals. Of all the tissues examined the oxygen consumption of isolated liver most closely reflected metabolic differences at the organismal level, both between taxonomic groups and in relation to body mass. (See Figs. 3.6 & 4.1).

4.3.4 The biochemical basis of the higher metabolic rates of mammalian tissues

The biochemical basis of the higher metabolic rate of mammalian tissues is not fully understood. However, it is known that the activities of some important mitochondrial enzymes are higher in mammalian tissues. Bennett (1972b) compared the activities of cytochrome oxidase, NAD-linked isocitrate dehydrogenase and succinic dehydrogenase in the liver and skeletal muscle of rats and three species of large lizards. It was found that the enzyme activities were 4 to 5 times greater in the mammalian tissues. Earlier studies on brain (Wahbe *et al*, 1961) and cardiac muscle (Robin & Simon, 1970)

reported that cytochrome oxidase activity was 2 and 6 times, respectively, greater in rat tissues that those from chelonians. In a comparative study of the laboratory mouse and the lizard *Amphibolurus nuchalis* Else & Hulbert (1981) found higher cytochrome oxidase activity in the liver, kidney, heart and brain of the mammal. This higher oxidative capacity of mammalian tissues appears to be related to the amount of mitochondria present, rather than qualitative differences in the enzymes themselves, since Mersmann & Privitera (1964) and Cassuto (1971) found isolated reptilian and mammalian mitochondria show similar enzymatic activities. This is supported by Else & Hulbert (1981) who used quantitative electron microscopy techniques to compare the mitochondrial content of mouse and *Amphibolurus* tissues. They found that in all four tissues examined the volume fraction of mitochondria was significantly higher in the mammal. In addition, the surface area of the inner mitochondrial membrane and cristae, in which the respiratory enzymes of the electron transport chain are located, is significantly greater in a given volume of mammalian mitochondria.

In liver tissue Bennett (1972b) found levels of mitochondrial enzyme activities to be around 3 to 5 times greater in mammals than reptiles, and Else & Hulbert (1981) reported a 2.69-fold difference in cytochrome oxidase activity. These values are comparable with the 3.5 to 4.5-fold differences in the metabolic rates of isolated liver tissue from rodents and lizards measured in the present study.

A higher oxidative capacity will not in itself result in mammalian tissues possessing higher respiration rates. This is because substrate oxidation does not normally proceed at its maximum rate, but is coupled to the ATP turnover of the cell. It is now generally

accepted that the energy release from substrate oxidation by the enzymes of the electron transport chain is used to extrude protons from the matrix of the mitochondrion. This allows energy to be stored as an electro-chemical gradient across the inner mitochondrial membrane, which is normally relatively impermeable to hydrogen ions. They are able to return to the matrix through the inner membrane spheres, where their stored potential energy is utilised to regenerate ATP. This explanation of the mechanism by which substrate oxidation is coupled to the phosphorylation of ADP is described as the chemi-osmotic model (Mitchell, 1967; Boyer *et al*, 1977). When no ATP is being produced oxidation proceeds only slowly, this idling level is described as state 4 respiration. However, as energy utilisation, and consequently ADP levels, in the cell rise there is a corresponding increase in the activity of the respiratory enzymes to restore the proton gradient depleted during the regeneration of ATP. The maximum respiration rate of which the mitochondria are capable is termed state 3. Normally the oxygen consumption of the mitochondria will be intermediate between states 3 and 4, the actual level depending on the ATP/ADP ratio within the living cell. The higher oxidative capacity of mammalian tissues will only be utilised if either their rate of ATP turnover is greater or phosphorylation is more loosely coupled to substrate oxidation, and therefore ATP is generated less efficiently from the proton gradient.

There are two ways in which the extrusion of protons could be uncoupled from the regeneration of ATP. First, the inner mitochondrial membrane could be made more permeable to protons, thereby establishing a futile cycle as protons would then return to the matrix without passing through the inner membrane spheres. This is thought to be the

principal thermogenic mechanism of mammalian brown fat, a tissue specialised to produce large amounts of heat (Nicholls, 1974), and is the mode of action of artificial uncoupling agents such as 2'4' dinitrophenol. Second, the energy stored by the proton gradient could be used for purposes other than ADP phosphorylation. One possible example is the uptake of calcium ions, for which mitochondria have a very high affinity, competes with phosphorylation for the energy released by substrate oxidation (Leninger, 1974). It has been suggested that this calcium ion uptake by mitochondria forms a component of the heat production in brown fat (Chriskansen, 1971; Linberg, Bieber & Houslek, 1975), although the contribution this makes to thermogenesis in other mammalian tissues is unknown. If any of these processes were operating in mammalian cells there would be a reduction in their ADP/O ratio, that is less ADP will be phosphorylated for a given amount of oxygen consumed. Although it is possible that in the biochemical environment of the intact cell mammalian mitochondria may operate at lower ADP/O ratios, *in vitro* studies indicate that this parameter is not very different in lower and higher vertebrates (Smith, 1973). However, it should be noted that the ADP/O ratios of isolated mitochondria are extremely sensitive to the particular experimental conditions used.

If the ADP/O ratios of reptilian and mammalian mitochondria are similar in the living cell then the higher oxygen consumption of the mammalian tissues must be due to a greater ATP turnover. The role of the Na^+-K^+-ATPase, the enzyme which maintains high intracellular K^+ and low Na^+ levels, in cellular thermogenesis has attracted particular attention. Several studies have implicated increased Na^+-K^+-ATPase activity, possibly under thyroid control, as an important component of

the increased BMR produced by cold acclimation in mammals (Ismail-Beigi & Edelman, 1970; Guernsey & Stevens, 1977; Guernsey & Whittow, 1980). It has been suggested that the higher metabolic levels of tachymetabolic than bradymetabolic vertebrates could similarly result from increased Na^+-K^+-ATPase activity (Stevens, 1973; Edelman, 1976). Using the Na^+-K^+-ATPase inhibitor ouabain Hulbert & Else (1981) estimated the contribution by this enzyme to the total energy metabolism of liver, kidney and brain in the mouse and *Amphibolurus nuchalis*. It was found that the absolute amount of energy utilised by the Na^+-K^+-ATPase was greatest in all three tissues from the mouse. Although it constituted a proportional increase in total cellular metabolism in liver and brain, in neither of these was the increased Na^+-K^+-ATPase activity sufficient to account for all of the higher metabolic rate of the mammalian tissues. However, there are many other important ATPases in the cell, although whether any of these also contribute to the higher levels of thermogenesis in mammals remains to be elucidated.

4.3.5 Summary

It is not possible to quantify precisely the increase in metabolic level which has taken place during the evolution of the modern eutherian mammals, even assuming that of their reptilian ancestors was within the range displayed by modern lizards. This is because the extent of the difference depends on both the species of reptile and mammal under comparison, and their body mass (Chapter 3.3.4). However, a typical small eutherian mammal , such as a 15 g rodent, has evolved a metabolic rate approximately 9 and 15 times greater than those of similarly sized lizards of the genera *Lacerta* and *Cordylus*, respectively. The acquisition of a mammalian metabolic

level was probably a gradual process, and a considerable degree of tachymetabolism may have already been evolved by the advanced mammal-like reptiles (Chapter 1.2). Indeed, it has been suggested that the thermoregulatory physiology of the living monotremes could be representative of the later cynodonts (Augee, 1978). An increase in SML during the evolution of the mammal-like reptiles may have been associated with the reduction in their body size observed in the fossil record (Chapter 1.2), possibly reflecting a shift from dependence on behavioural homeothermy and thermal inertia to endogenous heat production for the regulation of body temperature (McNab, 1978).

The higher metabolic levels of mammals are partly the consequence of a greater mass specific heat production by all of their body tissues. This increase in mammalian cellular metabolism, the extent of which varies considerably between tissues (Chapter 4.3.3), appears to be related to a greater density of mitochondria. The biochemical mechanisms utilised to release heat from this additional oxidative capacity are incompletely understood, although they may involve, at least in part, increased Na^+-K^+-ATPase activity (Chapter 4.3.4). However, whatever the biochemical basis of these differences at the cellular level it is clear that they are not sufficient to account for all of the higher metabolic levels of mammals. If the *in vitro* determinations of metabolism accurately reflect those of tissues in the living animals then additional factors must be contributing to the greater differences between reptiles and mammals at the organismal level.

One possible explanation is that the proportion of total body mass comprised of tissues with a relatively high oxygen consumption rate is greater in mammals than reptiles. This is supported by the finding of Else & Hulbert (1981) that liver, kidney, heart and brain together make up only 5.3% of total body mass in the lizard *Amphibolurus nuchalis*, compared with 10% in the mouse. Alternatively, it could be that tissues not represented in these *in vitro* studies are contributing to the higher metabolic levels of mammals. That such additional heat sources exist is indicated by comparisons of the metabolic rate of the mouse with those of its isolated tissues (Fig. 4.5a). Even although the intact animal also includes significant quantities of relatively metabolically inert substances, including fur, skin, bone and body fluids, its overall mass specific metabolic rate is not much lower than those of its more active component tissues, which make up only a small percentage of total body mass. Martin & Fuhrman (1955) also found that summated *in vitro* tissue respiration was less than that of the living mouse. It is possible that some of the additional heat could be produced by small localised thermogenic organs such as brown fat. This tissue, which has only been found in eutherian mammals (Hulbert, 1980b), is extremely rich in mitochondria which release large amounts of heat by the uncoupled oxidation of substrate (Smith & Horwitz, 1969; Himms-Hagen, 1976). Although brown fat is known to be important in thermoregulatory heat production, particularly for young mammals and hibernating species, it has not been shown to make a significant contribution to mammalian BMLs. The heat could also come from tissues examined in this study if their *in vitro* performance is markedly different from that in the living animal. An obvious candidate is the skeletal musculature,

which comprises a major proportion of total body mass in mammals (Martin & Fuhrman, 1955). As already discussed (Chapter 4.3.3), the very low oxygen consumption rate of this tissue *in vitro* is probably less than its metabolic rate in the living animal, where it may make a considerable contribution to BML (Krebs, 1950). The skeletal musculature is known to be important to the thermoregulatory responses of tachymetabolic animals during exposure to environmental temperatures below their thermoneutral zone (Jansky, 1965,1973,1977; Himms-Hagen, 1976). This additional heat is produced by shivering in all living mammals and non-shivering thermogenesis in marsupials and eutherians only (Hulbert, 1980b). It has been suggested that any higher muscular heat production by mammals under conditions of thermoneutrality could be associated with the postural differences between them and the reptiles (Heath, 1968). In contrast to the sprawling gait of reptiles, mammals possess an upright posture in which the limbs are held directly beneath the body, thereby lifting it clear of the ground. The constant muscle tonus required to support the body in this position should generate additional metabolic heat, even while the animal is stationary. This could also explain why *Chamaeleo chamaeleon* displayed the highest SML of all the species of lizards examined in the present study. Therefore, although the higher metabolic levels of mammals have probably been primarily achieved by a general increase in metabolism at the cellular level combined with a reduction in the proportion of the body composed of less metabolically active tissues, the heat production resulting from increased muscle tonus may also have been a contributory factor.

CHAPTER 5

ACCLIMATION TO THERMAL ENVIRONMENT IN LIZARDS

5.1 INTRODUCTION

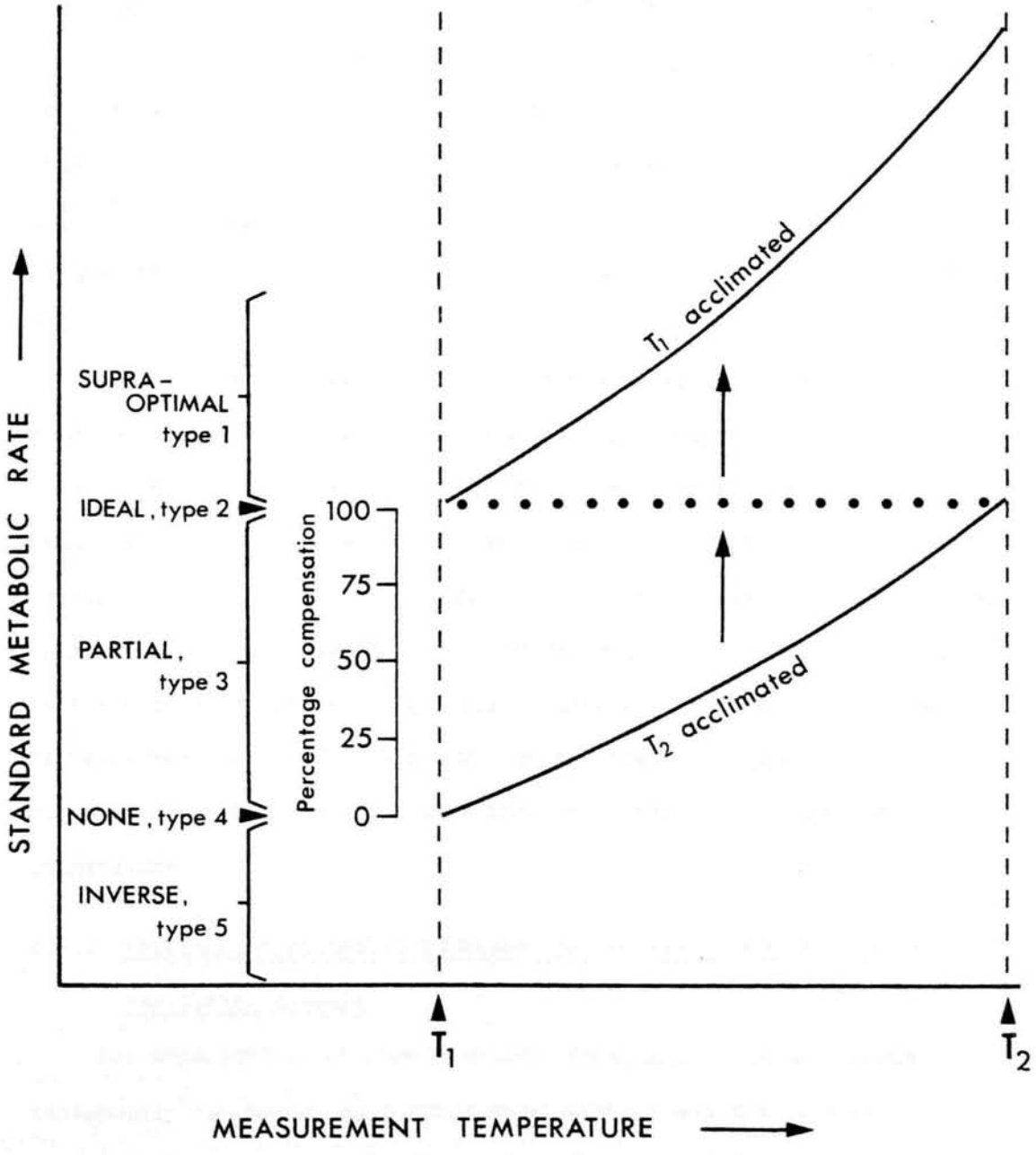
5.1.1 Metabolic acclimation in bradymetabolic animals

Most bradymetabolic organisms are able to adjust their biochemistry and physiology in response to long-term fluctuations in environmental conditions. These non-genetic changes in phenotype are often termed acclimatisations, when they occur in organisms living under natural conditions, or acclimations if produced under controlled laboratory conditions and can be attributed to the influence of a specific variable. Acclimatory responses can modify the limits of a particular variable which an organism is able to tolerate, or act to restore the normalised functioning of rate processes which would otherwise be perturbed by alterations in environmental conditions. It is the latter compensatory acclimations of reptilian standard metabolic rates (SMRs) to environmental temperature with which this study is concerned.

When a lower vertebrate or invertebrate is moved from one temperature regime, T_2, to a cooler one, T_1, it will initially experience a reduced SMR (Fig. 5.1). As discussed in Chapter 2.3.3, the Q_{10} values of this temperature dependency of oxygen consumption in lizards typically lie between 2 and 3. If after prolonged exposure to T_1 metabolic rate, measured at T_1, remains unaltered at this new low level then no capacity acclimation has occurred. This is referred to as a type 4 acclimatory response (Precht *et al*, 1973). More often the temperature dependency curve become shifted, restoring oxygen consumption towards its pre-acclimatory level measured at the original

Figure 5.1 The influence of environmental temperarure (T_e) on the standard metabolic rate of a bradymetabolic organism acclimated to two different environmental temperatures of T_1 and T_2 (for explanation see text 5.1.1).

Fig. 5.1


STANDARD METABOLIC RATE
SUPRA-OPTIMAL type 1
IDEAL, type 2
PARTIAL, type 3
NONE, type 4
INVERSE, type 5
Percentage compensation
100
75
50
25
0
T_1 acclimated
T_2 acclimated
T_1
T_2
MEASUREMENT TEMPERATURE

temperature, T_2. This compensation may be partial (type 3), or ideal (type 2) if an animal acclimated and measured at T_1 completely regains the SMR it had when acclimated and measured at T_2. The extent to which partial acclimation restores SMR to that prevailing under the original temperature regime can be expressed as a percentage. For example, an organism will be 50% compensated if the SMR of the animal acclimated and measured at T_1 returns half way to its original level acclimated and measured at T_2. Occasionally compensation may exceed 100%, or ideal (type 2) acclimation, and become supra-optimal (type 1). The final possibility is that following acclimation SMR shifts even further from its original level, a condition known as inverse (type 5) compensation.

Acclimation to changes in environmental temperature have been demonstrated in a wide range of bradymetabolic species (Precht, *et al*, 1973). The mechanisms of these changes are incompletely understood, but are known to involve alterations of enzyme activities (Hazel & Prosser, 1970, 1974) and modifications of membrane biochemistry (Johnston & Roots, 1964; Caldwell & Vernberg, 1970). The time courses of these changes are variable, usually occurring in the order of days to weeks (Precht *et al*, 1973). Therefore, these responses are compensations to seasonal, rather than short-term daily, changes in temperature.

5.1.2 Problems of metabolic compensation for behaviourally thermoregulating animals

For organisms which remain active throughout the year and are continually isothermal with their environment there are obvious advantages in partial (type 3) or ideal (type 2) shifts in metabolism

to maintain some degree of homeostasis in the face of long-term changes in temperature. However, for some bradymetabolic animals, including reptiles, which behaviourally thermoregulate the situation is more complex. Although for most of each 24-hour period the body temperature of a lizard will correspond closely to that of its surroundings, during activity many species maintain some degree of homeothermy. This is achieved primarily by behavioural responses, such as shuttling between microclimates of differing temperature and postural changes (Cowles & Bogert, 1944; Heath, 1965, 1970), although it also involves some physiological mechanisms, including control of the peripheral circulation (Bartholomew & Lasiewski, 1965; Bartholomew, 1966, Morgareidge & White, 1969), evaporative cooling from the upper respiratory tract and buccal cavity (Webb & Johnson, 1972; Crawford, 1972), and even changing the albedo of the skin through the action of melanophores (Parker, 1906; Cole, 1943; Norris, 1967). The mean body temperature the members of a species select when placed in a laboratory temperature gradient is called preferred body temperature (PBT). This may differ from the mean body temperatures of active lizards in the field since these are often a compromise between the preferred value and that actually attainable in a given thermal environment.

Although this daily period of homeothermy provides the animal with the advantages of short-term temperature stability it introduces considerable complexities when its relationships with long-term changes in environmental temperature are considered. If it remained isothermal with its surroundings at all times then acclimation would afford the advantages of the increased metabolic homogeneity already discussed. Conversely, if these reptiles were able to regulate continually at a constant body temperature then no acclimation would take place, or be

required. However, regulating body temperature for only part of each 24-hour cycle and becoming isothermal with their surroundings for the remainder, presents lizards with a problem. If they acclimate to compensate for changes in the environmental temperatures they experience during their inactive phase this will cause unwanted shifts in SMR during the period each day the lizard continues to regulate at its PBT. Therefore the acclimatory responses of these reptiles could follow one of several patterns.

1) The lizard exhibits metabolic acclimation (either partial, type 3, or ideal, type 2) *and* alters its PBT

   This strategy has the advantage of both increasing homeostasis during the animal's inactive phase and still maintaining an unchanged SMR while it is thermoregulating. For example, a long-term lowering of environmental temperature would initially cause a fall in metabolism during the lizard's inactive phase. Through acclimation the animal compensates by elevating its SMR. An undesirable consequence of this is that if the animal continues to regulate at its original PBT then its SMR during this period will be elevated above its normal level. However, this could be prevented by lowering the PBT by the amount necessary to retain the original metabolic rate.

or, 2) The lizard exhibits metabolic acclimation (either partial, type 3, or ideal, type 2) but its PBT remains fixed.

   This response only achieves any compensation during the inactive phase at the expense of an altered metabolic rate while the lizard is thermoregulating. Adoption of this strategy would indicate that a homogeneous SMR is not of crucial importance to the lizard during its active phase.

or, 3) The lizard maintains both a fixed SMR (type 4 acclimation) and PBT.

Although by suppressing acclimation a constant metabolic rate is always maintained during behavioural thermoregulation at the PBT, any long-term fluctuations in environmental temperature will cause corresponding changes in SMR during the rest of each 24-hour period. Such a response would indicate that metabolic homogeneity is of greatest importance to the animals while they are active.

The objective of Experiment 1 was to establish which of these possible acclimatory responses occurs in lizards. This was investigated by determining whether shifts in PBT, SMR,or both occur in experimental animals maintained under different constant temperature regimes.

Although this experiment should establish the potential for acclimation of SMR under controlled conditions, whether this actually occurs under natural conditions could be further complicated. As already discussed the body temperature of a wild lizard may vary considerably throughout each 24-hour period. For exmaple, while thermoregulating a lizard might maintain a temperature of around 35°C but during its inactive phase this could fall to 10 to 20°C. It is therefore important to establish to which of the range of temperatures it experiences the animal actually becomes acclimated. For instance, lizards might be capable of considerable shifts in SMR when acclimated under a constant temperature regime, but this potential would not be utilised under natural conditions if they remained acclimated to their fixed PBT. To establish whether lizards become acclimated to the body temperatures they experience during their active phase (PBT), inactive phase (T_e)

or some intermediate value, a second experiment was conducted. Groups of lizards were acclimated to 20 and 30°C which also had access to a radiant heat source during the day. Therefore, they could behaviourally thermoregulate at their PBT during the day and their body temperature during their inactive phase was known. After the period of acclimation the SMRs of both groups were compared with control animals which had been acclimated isothermally at the two temperatures.

5.2 MATERIALS AND METHODS

5.2.1 Animals

Two species of small lizards were used; a temperature European lacertid, *Lacerta lilfordi* (melanistic phase), and a tropical African cordylid, *Cordylus jonesi*. Sufficient adults of these two species were avialable to allow groups of animals to be maintained under various acclimatory regimes.

Before commencing experiments all lizards were housed, fed and maintained under the standard conditions already described in Chapter 2.2.1.

5.2.2 Determination of preferred body temperature (PBT)

Experimental animals were placed in a thermal gradient, within which they were free to move and regulate their body temperature by behavioural means. The thermal gradients were established in large stainless steel tanks, measuring approximately 100 x 50 x 50 cm. These contained a 3 to 6 cm deep gravel substrate, on which wood and rocks were arranged to provide suitable retreats for the reptiles. To produce a temperature gradient along the tank two 100 W tungsten light bulbs were mounted in reflectors and positioned approximately 20 cm above the substrate at one end. The tanks were evenly illuminated by a mixture of natural daylight, although not direct solar radiation, and fluorescent strip lights. It was necessary to ensure that the range of temperatures within the gradient extended well above and below the PBT of the lizards. The temperatures at the substrate surface, measured with a thermistor, ranged from 1 to 3°C above room temperature (usually approximately 20°C) in the shade at the cooler end of the gradient, to in excess of 60°C directly below the radient heat source. Water was

available to the lizards at all times during experiments, and small quantities of livefood were introduced into the tanks at intervals throughout the day. The tanks were located in a quiet room to minimise noise and visual disturbance.

For determinations of PBT the lizards were introduced to the gradients soon after the start of their normal photophase. A maximum of six lizards were placed in a tank during an experiment. Individuals were identified by small markings applied to the undersurface of the base of the tail with nail varnish. The animals were left undisturbed for the first two hours. Throughout the following 6 hours all individuals were removed at 40 to 60 minute intervals and their body temperatures measured. A maximum of five readings were made from a single animal during the course of an experiment. Considerable care was taken to remove the lizards from the tank with minimal disturbance, since errors would result if animals which had not yet been measured were displaced to warmer or cooler regions of the gradient.

Body temperature determinations were made using an expoxy resin encapsulated thermistor and an electronic thermometer constructed to the specification of Laws (1977). This instrument allows measurements to be made quickly to an accuracy of ± 0.1°C. To take readings of body temperature the thermistor was inserted into the cloaca of the lizard to a depth of 1 to 3 cm, depending on the size of the individual.

It was found in preliminary experiments that the measurements taken during an experiment were not all normally distributed, but that there were two distinct maxima. Observations of marked animals showed that the reason for this was that not all individuals regulated continuously throughout the day. Resting lizards were not distributed randomly along the gradients but had moved to the cooler regions of the

tanks, thereby producing the smaller lower peak. Regal (1967) observed similar behaviour working with lizards in artificial thermal gradients. The higher cluster of measurements, which are more normally distributed, represented the body temperatures of actively thermoregulating individuals. If the temperature of the cooler regions within the gradient is sufficiently below the PBT of the lizards the two clusters of measurements can be completely separated. All results quoted in this study are means calculated from the higher peak, and therefore represent the body temperatures of actively thermoregulating lizards only.

5.2.3 Determination of standard metabolic rate (SMR)

With the exception of differences in measurement temperatures, all determinations were made using the same equipment and procedures described in Chapter 2.2.2.

5.2.4 Experimental procedures

Experiment 1: Acclimation of PBT and SMR to temperature in lizards maintained under isothermal conditions

Groups of both species were isothermally acclimated to environmental temperatures of 30 or 20°C. The two groups of *Lacerta lilfordi* each contained eight individuals, and the *Cordylus jonesi* groups ten animals. Within both species the sizes of lizards in each group were matched as closely as possible to reduce errors introduced by the body mass dependency of SMR. During the acclimation period the lizards were housed in large plastic tanks containing a gravel substrate and rocks to provide suitable retreats. Drinking water was continually available and they received normal quantities of food except for the five days before measurements of SMR were made, when none was given.

The tanks were placed in a large environmental chamber where ambient temperature could be accurately controlled and monitored. All groups were maintained on a 12 L:12 D photoperiod, the photophase commencing at 08.00 GMT.

Prior to the experimental acclimation all animals were initially acclimated to a standard temperature of 30°C for 8 weeks. After this preliminary period one group of each species remained at 30°C and the other was placed in a separate chamber at the lower temperature of 20°C. The lack of any radiant heat source forced the lizards to remain isothermal with their respective environmental temperatures at all times. After 3, 5 and 7 weeks from the start of the second acclimation period the PBT of each group was determined in the thermal gradients. Between weeks 5 and 7 the SMR of each lizard was measured at both 20 and 30°C.

Experiment 2: Acclimation of SMR to temperature in behaviourally thermoregulating lizards

For this experiment four groups of *Cordylus jonesi* were used, each consisting of six lizards maintained under the conditions described for Experiment 1. After preliminary acclimation to 30°C for 8 weeks two groups were isothermally acclimated at 20 and 30°C. A further two groups were acclimated at these temperatures and provided with an additional radiant heat source during their photophase to enable them to behaviourally thermoregulate. This consisted of a 60 W tungsten light bulb mounted in a reflector placed over one end of the tank. The temperature of the substrate immediately below the bulb was raised to more than 45°C, while the cooler areas of the tank remained approximately isothermal with the room. The radiant heat source was switched on for

the middle 8 hours of each 12 hour photophase. After five weeks exposure to the appropriate acclimatory regime the SMR of all lizards was determined at 30°C.

5.3 RESULTS

5.3.1 Experiment 1: Acclimation of PBT and SMR to temperature in lizards maintained under isothermal conditions

Both species behaviourally thermoregulated when placed in a thermal gradient (Figs. 5.2 & 5.3). The mean body temperatures of active lizards of the two species are presented in Table 5.1. The differences between the PBTs of *Lacerta lilfordi* maintained at 20 and 30°C were not significant after 5 and 7 weeks ($P > 0.05$), although the slight difference of 0.9°C at week 3 was significant ($P < 0.05$). No significant differences in PBT were found between 20 and 30°C acclimated *Cordylus jonesi* at any stage ($P > 0.05$). Therefore long-term acclimation to temperature has not shifted the PBT of either species.

The SMRs of the two species acclimated to 20 and 30°C are shown in Table 5.2 and Fig. 5.4. The SMRs of *Lacerta lilfordi* acclimated to 20°C were higher than those maintained at 30°C at both measurement temperatures, although the difference was only significant at 20°C ($P < 0.05$). The *Cordylus jonesi* acclimated to 20°C possessed significantly higher SMRs than the 30°C acclimated group at both 20°C ($P < 0.05$) and 30°C ($P < 0.001$). Therefore the oxygen consumption rates of both species have acclimated in response to a change in their thermal environment. These shifts in SMR are equivalent to partial (type 3) compensations of 10.5% in *Lacerta lilfordi* and 20.9% in *Cordylus jonesi*. Thermal acclimation did not affect the Q_{10} value of either species.

Table 5.1 The preferred body temperature (PBT) of lizards acclimated to environmental temperatures of 20 and 30°C

Species		PBT, °C					
		WEEK 3		WEEK 5		WEEK 7	
		mean ± S.E.	n	mean ± S.E.	n	mean ± S.E.	n
Cordylus jonesi	20°C acclimated	33.3 ± 0.3	37	34.0 ± 0.2	55	33.6 ± 0.2	44
	30°C acclimated	33.4 ± 0.3	47	33.4 ± 0.4	32	33.7 ± 0.3	50
	Comparison (t-test)	N.S.		N.S.		N.S.	
Lacerta lilfordi	20°C acclimated	34.1 ± 0.3	44	34.5 ± 0.4	34	33.5 ± 0.2	34
	30°C acclimated	33.2 ± 0.3	46	33.8 ± 0.4	30	34.2 ± 0.3	40
	Comparison (t-test)	$p < 0.05$		N.S.		N.S.	

Figures 5.2 & 5.3 Frequency histograms of the cloacal temperatures of active lizards following acclimation to environmental temperatures of either 20°C or 30°C for 3, 5 and 7 weeks. The PBTs quoted in Table 5.2 are the means of of these values.

Figure 5.2 *Lacerta lilfordi*

Figure 5.3 *Cordylus jonesi.*

Fig. 5.2 LACERTA LILFORDI

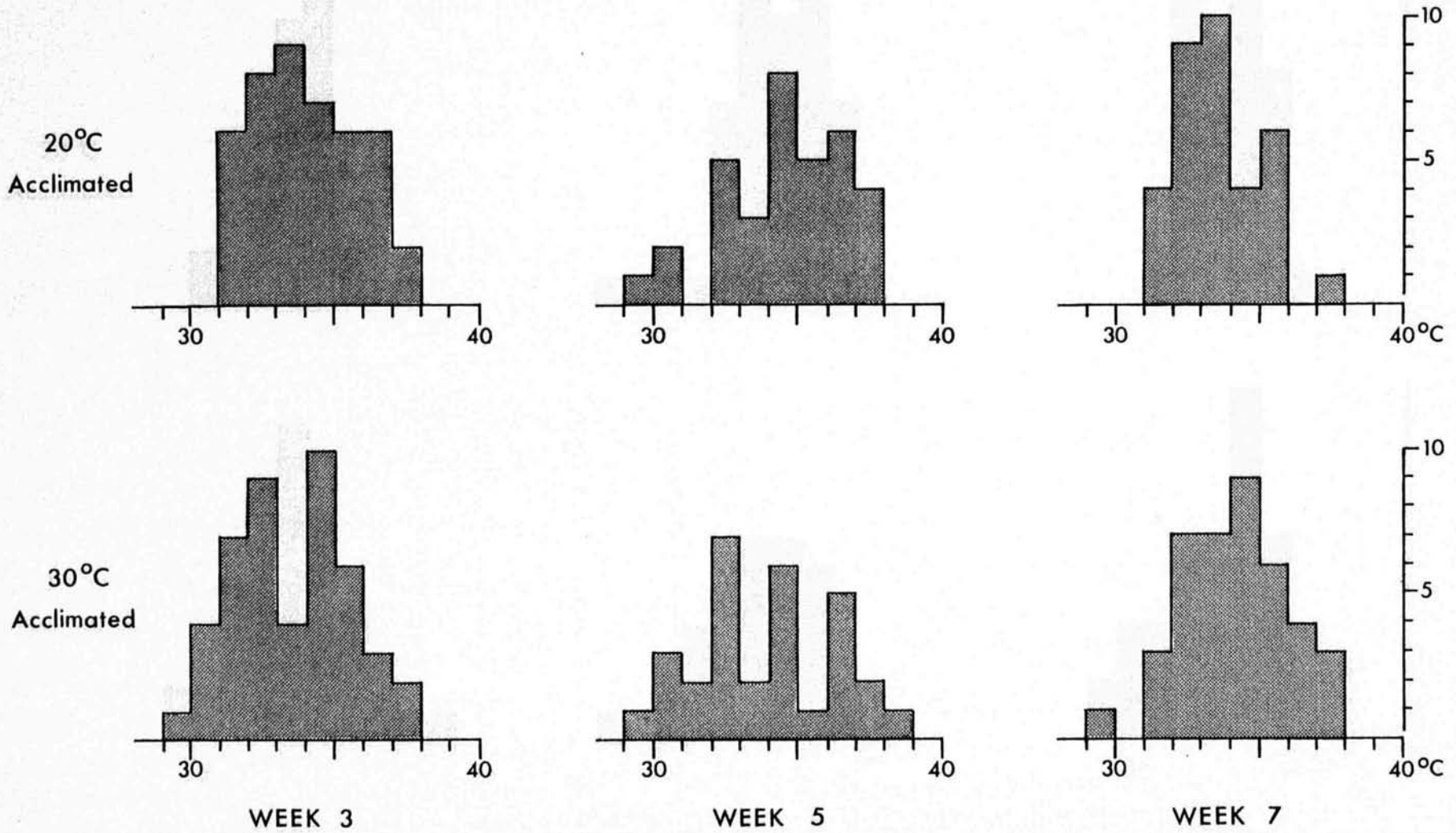


Fig. 5.3 CORDYLUS JONESI

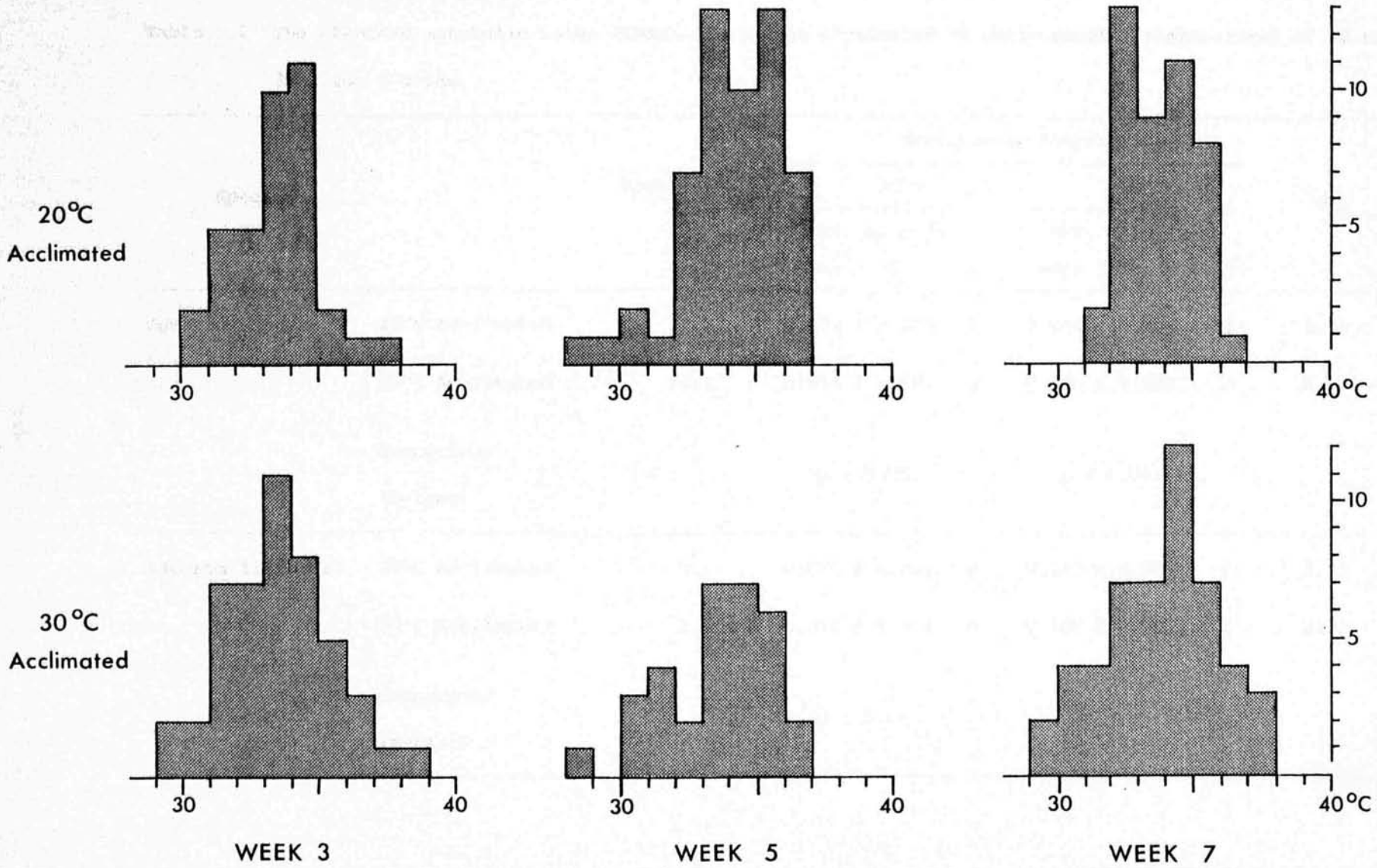
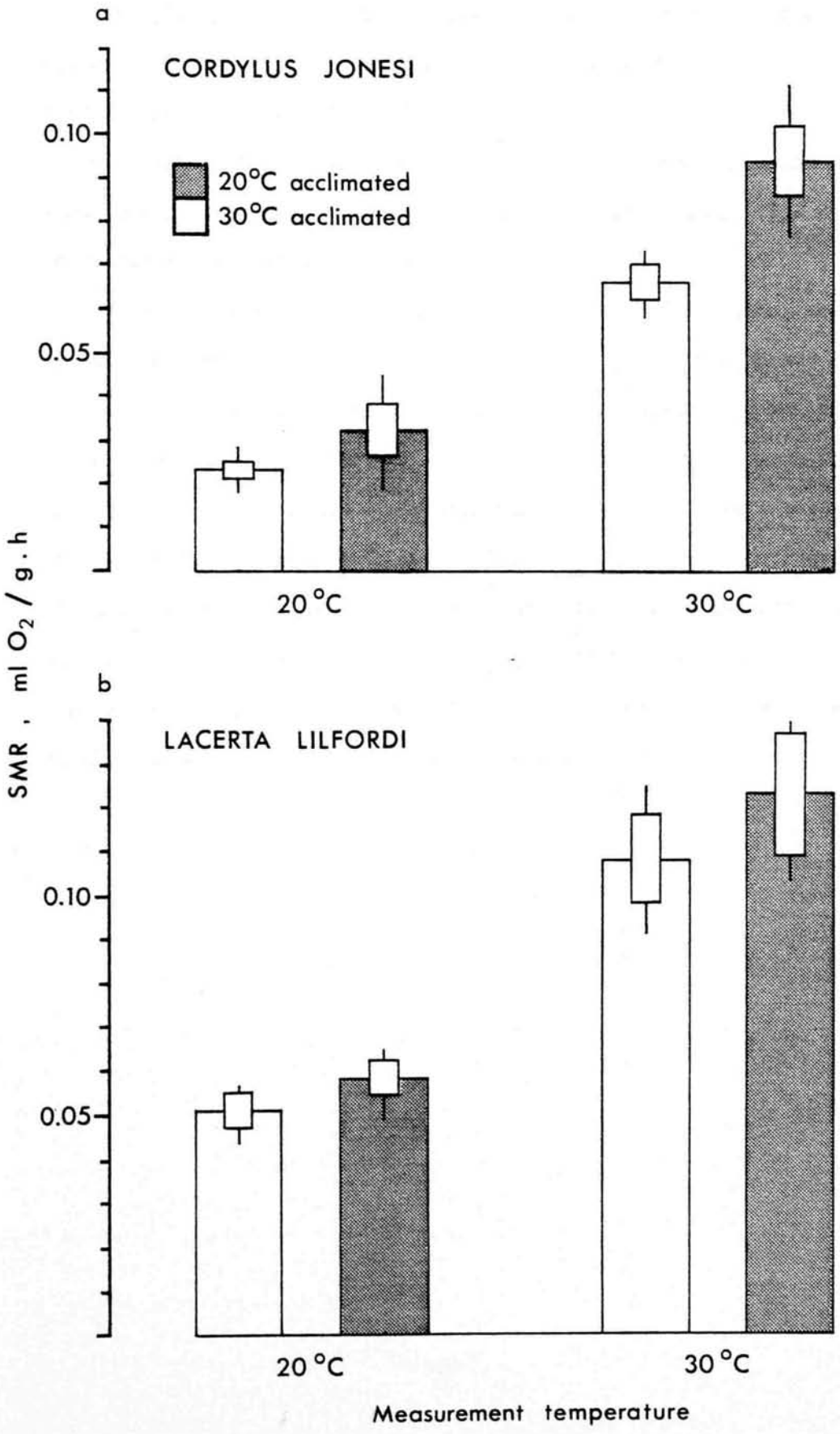


Table 5.2 The standard metabolic rates (SMRs) of lizards acclimated to environmental temperatures of 20 and 30°C for 5 weeks.

Species		Body mass, g mean	Measurement temperature				Q_{10}
			20° C		30 °C		
			SMR, ml O_2/g.h		SMR, ml O_2/g.h		
			mean ± SE	n	mean ± SE	n	
Cordylus jonesi	20°C Acclimated	12.1	0.032 ± 0.003	8	0.094 ± 0.004	8	2.94
	30°C Acclimated	12.1	0.023 ± 0.001	8	0.066 ± 0.002	8	2.87
	Comparison (t-test)		$p < 0.05$		$p < 0.001$		
Lacerta lilfordi	20°C Acclimated	9.7	0.057 ± 0.002	6	0.123 ± 0.007	6	2.12
	30°C Acclimated	8.7	0.051 ± 0.002	6	0.108 ± 0.005	6	2.12
	Comparison (t-test)		$p < 0.05$		N.S.		

Figure 5.4 Mean mass specific standard metabolic rates of (a) *Cordylus jonesi*, and (b) *Lacerta lilfordi*, following 5 weeks acclimation to either 30°C (open) or 20°C (shaded) at measurement temperatures of 20°C and 30°C. Rectangles represent ± 2 S.E. and bars the range (see Table 5.2).

Fig. 5.4


a
CORDYLUS JONESI
20°C acclimated
30°C acclimated
0.10
0.05
20 °C
30 °C
b
LACERTA LILFORDI
0.10
0.05
20 °C
30 °C
SMR , ml O_2 / g . h
Measurement temperature

5.3.2 Experiment 2: Acclimation of SMR to temperature in behaviourally thermoregulating lizards

Cordylus jonesi acclimated to background temperatures of 20°C possessed significantly higher SMRs than those maintained at 30°C in both radiantly heated ($P < 0.001$) and isothermal control ($P < 0.05$) groups (Table 5.3 & Fig. 5.5). Therefore both thermoregulating and isothermally acclimated lizards show evidence of partial (type 3) compensation between 20 and 30°C.

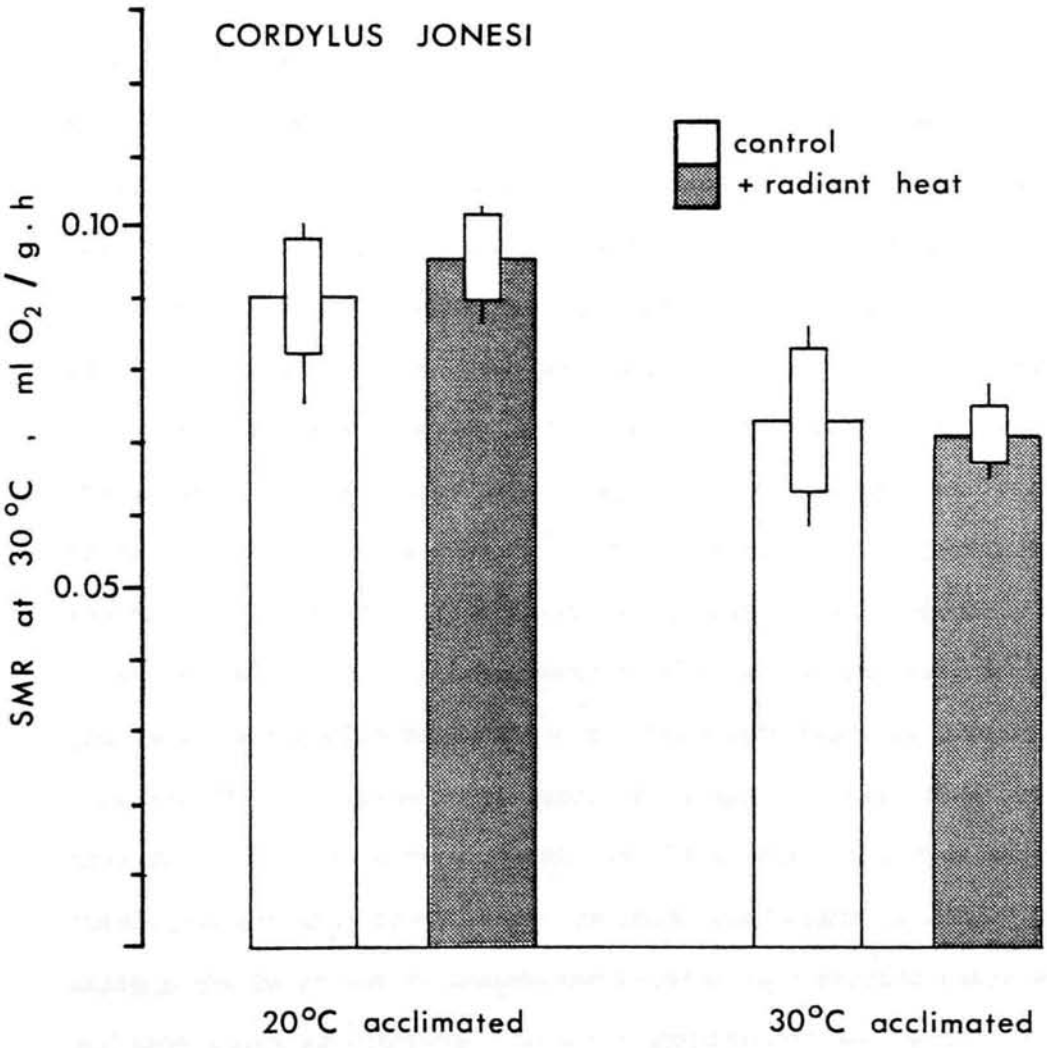
If the lizards in the radiantly heated groups had become acclimated to the temperature they experienced during the resting phase then their SMRs should be the same as those animals continually maintained at that temperature. However, if they acclimate to their PBT, which is higher than both background temperatures used, or some intermediate value then the SMR of the thermoregulating groups should be lower than the appropriate isothermal control group. At both 20 and 30°C there was no significant difference between radiantly heated and control groups ($P > 0.05$), indicating that the lizards had become acclimated to the temperatures they experience while at rest.

Table 5.3 The standard metabolic rates (SMRs) measured at 30°C of *Cordylus jonesi* acclimated to environmental temperatures of 20 and 30°C for 5 weeks. Controls were isothermally acclimated to the appropriate temperatures and experimental animals had access to a radiant heat source for 8 hours during their photophase.

Acclimation temperature	Body mass, g. Mean	SMR, ml O_2/g.h mean ± SE	n
20°C, control	13.0	0.090 ± 0.004	6
20°C, + radiant heat	11.6	0.096 ± 0.003	6
Comparison (t-test)		N.S.	
30°C, control	13.9	0.073 ± 0.005	5
30°C, + radiant heat	14.3	0.071 ± 0.002	6
Comparison (t-test)		N.S.	

Figure 5.5 Mean mass specific standard metabolic rates of *Cordylus jonesi* measured at 30°C following 5 weeks acclimation to either 20 or 30°C. Controls (open) were maintained isothermally at the appropriate temperature and experimental groups (shaded) had access to a radiant heat source for 8 hours during their photophase. Rectangles represent ± 2 S.E. and bars the range (see Table 5.3).

Fig. 5.5


CORDYLUS JONESI
control
+ radiant heat
SMR at 30 °C , ml O_2 / g . h
0.10
0.05
20°C acclimated
30°C acclimated

5.4 DISCUSSION

5.4.1 Acclimation of lizard PBTs to environmental temperature

The results obtained in this study show that isothermal acclimation to 20 or 30°C does not alter the PBT of either *Lacerta lilfordi* or *Cordylus jonesi*. There have been few previous studies investigating the effect of temperature acclimation on the PBTs of lizards under controlled laboratory conditions. Licht (1968) also found that acclimation state does not alter the PBT of *Anolis carolinensis* . However, Wilhoft & Anderson (1960) reported that exposure of *Sceloporus occidentalis* to high ambient temperatures could reduce their PBT, the opposite of what would be expected in a compensatory response.

The effect of seasonal acclimatisation on the mean body temperatures of wild lizards has been examined by several workers. After measuring the body temperatures of active *Sceloporus orcutti* in the field throughout the year Mayhew (1963) reported that the mean was significantly lower during the winter. However, Stebbins (1963) found that seasonal differences did not exist if the PBTs of wild-caught *Sceloporus virgatus* were determined in the laboratory using a thermal gradient. A possible explanation for this difference in findings is that the PBT of lizards is unaltered by seasonal acclimatisation and they will continue to regulate at that level when they have access to sufficient radiant energy, as in the laboratory gradient. However, wild animals may be forced to compromise between this desired temperature and that which is attainable in their environment during the cooler months of the year. This was confirmed by McGinnis (1966) who measured the body temperature of wild surface-active *Sceloporus occidentalis* throughout the year and also determined their PBT after capture by

placing them in a laboratory thermal gradient. It was found that although the mean body temperatures of lizards in the field was lowest in winter, when the animals were placed in the gradient there were no observed seasonal differences in PBT.

Patterson & Davies (1978a) have reported some differences in the PBTs of seasonally acclimatised *Lacerta vivipara* when measured in a temperature gradient. Interestingly, these fluctuations in PBT do not correlate with environmental temperature. For example, PBTs are higher in the spring and autumn than during the summer. These workers suggest that the changes, which are different in the male and female, may be related to the reproductive physiology of these viviparous lizards.

5.4.2 Acclimation of lizard SMRs to environmental temperature

There are no previous studies on cordylids with which the 20.9% partial compensation of *Cordylus jonesi* can be compared. Acclimation in lacertids was investigated by Gelineo & Gelineo (1955a, b). This work reported 50% compensation in *Lacerta muralis* and *L. sicula*, and complete compensation in *L. oxycephala* and *L. melisellensis*. These values are considerably higher than the 10.5% partial compensation found in the closely related *L. lilfordi* by the present study, and include the only reported examples of complete (type 2) compensation in reptiles. However, the metabolic rates quoted in these studies are abnormally high and there is considerable doubt that they represent true resting levels (Bennett & Dawson, 1976). Therefore, these results must be viewed with caution until the acclimatory responses of these species have been re-examined.

Studies on other families have shown varying degrees of compensation in lizards acclimated isothermally under laboratory conditions.

After maintaining *Urosaurus ornatus* at 8 and 35°C, Vance (1953) found significantly higher metabolic rates in the low temperature acclimation group when both were subsequently measured at 15°C. Murrish & Vance (1968) found approximately 25% compensation between groups of *Uta mearnsi* acclimated at 15 and 35°C for about ten days. Maher & Levedahl (1959) reported 50% compensation in *Anolis carolinensis* within three weeks, although Ragland, Wit & Sellers (1981) found only 3.8% compensation between lizards of this species maintained at 10 and 30°C for two weeks. There are also considerable differences in the results of studies on lizards of the genus *Sceloporus*. Dawson & Bartholomew (1956) found a shift in the metabolism of *Sceloporus occidentalis* corresponding to approximately 8% compensation, although Bartlett (1970) reported no evidence of acclimation to temperature by this species. Experiments with *S. olivaceous* by Dutton & Fitzpatrick (1975) showed 71% compensation between lizards acclimated at 20 and 30°C. Although this value is high it should be noted that the experimental procedures used in this study do not allow the effects of temperature to be separated from photoperiod differences experienced by the lizards. Therefore, when maintained at differing constant body temperatures for a few weeks many species of lizards have been shown to possess the capacity to compensate metabolically, although the extent of this acclimatory response appears to vary considerably.

In the second experiment it was found that the SMRs of *Cordylus jonesi* which had access to a radiant heat source were not significantly different from those of lizards acclimated isothermally to the same background temperatures of 20 and 30°C. This demonstrates that even if the lizards are maintaining a constant body temperature for part of each day their capacity for metabolic compensation is still utilised, and

they have become acclimated to the prevailing environmental temperature. This could be because either the acclimatory response is suppressed during the lizards' active phase or, more likely, that the animal is thermoregulating for too small a proportion of each 24-hour period for this to be a significant influence on its acclimatory state.

Data from wild caught, seasonally acclimated, lizards indicate that metabolic compensation does take place under natural conditions. Roberts (1968) found that during the winter months *Uta stansburiana* had a resting metabolic rate between 25 and 35°C that was 20% lower than in summer, however, Morris (1981) found no evidence of compensation in the skink *Leiolopisma zelandica*. In *Sceloporus olivaceous*, Dutton & Fitzpatrick (1975) found that lizards from environmental temperatures close to 15°C had significantly higher metabolic rates than those collected at the higher temperatures of 20, 25 and 30°C, although the degree of compensation was generally less than in laboratory acclimated animals maintained at comparable temperatures.

This contrasts with the situation in the closely related *S. occidentalis* (Heusner & Jameson, 1981). Oxygen consumption rates in this species reached in maximum in May-June and then subsequently declined through the fall. Similar inverse (type 5) compensation has been reported in four species of temperate European lizards (Patterson & Davies, 1978b). In this study groups of *Lacerta hispanica*, *Psammodromus hispanicus*, *Lacerta vivipara* and *Anguis fragilis* were acclimated to a range of environmental temperatures, with access to a radiant heat source for part of each day. Unlike the present study the photoperiod and duration of radiant heating also varied between groups. Therefore, these regimes should be considered as seasonal, rather than

thermal, acclimations. Inverse compensation also appears to be a widespread response among reptiles hibernating under natural conditions (Moberly, 1963; Mayhew, 1965; Aleksiuk, 1976; Patterson & Davies, 1978c). It can be interpreted as a strategy for conserving energy, either during dormancy or the preceding period of fat accumulation, in species which do not remain continually active throughout the year. Ragland, Wit & Sellers (1981) contrasted the metabolic responses of *Anolis carolinensis*, which is periodically active throughout the winter, with *Cnemidophorus sexlineatus*, a hibernator. They found that wild-caught, hibernating, *C. sexlineatus* displayed inverse (type 5) compensation, whereas *A. carolinensis* acclimated to lower temperatures with partial (type 3) compensation. Inverse compensation in lizards appears to be induced by factors in addition to environmental temperature change alone, since all the studies in which it has been reported involved animals living in natural conditions or under experimental regimes in which photoperiod was also manipulated. Indeed, when *C. sexlineatus* was acclimated to temperature only, under laboratory conditions, no shift in metabolism took place (Ragland, Wit & Sellers, 1981).

5.4.3 Summary

Lizards, like most other bradymetabolic vertebrates, have the capacity to acclimate the resting metabolic levels when maintained at different constant body temperatures. In species which remain active throughout the year the response is usually partial (type 3) compensation, although the extent of this is relatively low and varies considerably between both species and studies. This potential to acclimate is utilised even if the lizards continue to thermoregulate at their PBT

for part of each day. Metabolic compensation occurs naturally during seasonal acclimatisation, although this may be less than when thermal acclimatisation is induced under controlled laboratory conditions. In contrast, hibernating lizards under natural conditions often display inverse (type 5) compensation, a strategy which probably facilitates energy conservation during the period of dormancy. This latter response is probably only induced by the combined influences of temperature and photoperiod changes.

The PBTs of most species examined appear to be relatively fixed, although in the wild the mean body temperatures of active lizards may fluctuate during the year as they are forced to compromise with seasonally changing environmental temperatures. Therefore, lizards do not maintain complete metabolic homeostasis in either their active or resting phases. Since the extent of the compensation is relatively small, usually much less than 50%, metabolism will be more stable on a seasonal basis during the period the animal is behaviourally thermoregulating. Complete metabolic homeostasis can only be achieved during activity by a compensatory reduction in PBT. For example, following a reduction in environmental temperature from 30 to 20°C *Lacerta lilfordi* would need to lower its PBT by approximately 1.4 °C, and *Cordylus jonesi* by 4.1°C, to compensate for their respective metabolic acclimations. The required shifts were not observed in the PBTs measured in a thermal gradient. However, in the wild all or part of this reduction in PBT may be imposed on the lizards during the cooler months of the year by the lower environmental temperatures.

This does not explain why lizards still attempt to maintain an unaltered PBT, even though this is disadvantageous in terms of metabolic homeostasis. It could be that it is not physiologically

possible to modify the set points of the neuronal networks responsible for behavioural thermoregulation. Another possibility is that physiological processes which require the maintenance of a constant fixed PBT are more important to the lizard than complete metabolic homogeneity. Possible examples of this could be the functioning of the neuromuscular and central nervous systems (see Chapter 6.4.3).

CHAPTER 6

ADAPTATION TO THERMAL ENVIRONMENT IN LIZARDS

6.1 INTRODUCTION

Although diurnal warm temperate and tropical species are predominant, lizards are found in a wide range of habitats from the equator to inside the Arctic Circle. An important question is whether the metabolic levels of reptiles have undergone any evolutionary compensation to their thermal environment. Such genetic changes are termed adaptations, as distinct from the acclimations of phenotype discussed in Chapter 5. Adaptations of metabolic rate have been reported in a wide range of aquatic bradymetabolic organisms including molluscs (Thorsen, 1952), crustaceans (Vernberg & Costlow, 1966; Vernberg & Vernberg, 1966) and fish (Brett , 1971); species from cooler climates possessing higher metabolic levels to compensate for the lower temperatures at which they must operate. Therefore, within taxa the rates of oxygen consumption of species from different environments are more similar, when measured at the temperature of their respective habitats, than a normal Q_{10} relationship would predict.

Such adaptations are not unexpected in these aquatic organisms which are continually isothermal with their surroundings. The situation may be different in reptiles where the relationships between body temperature and that of their environment is not as simple. Terrestrial habitats are considerably more heterogeneous, affording lizards a range of different thermal microclimates within a given environment. The situation is further complicated by most species regulating their body temperature above that of their surroundings for part of each day. Therefore, any adaptive trends among reptiles could be considerably

more complex than those found in aquatic temperature conformers.

Bennett & Dawson (1976) looked for evidence of adaptation in reptilian metabolism by examining the relationship between oxygen consumption and PBT. They concluded that no adjustment had occurred in the species examined. However, this does not exclude the possibility that adaptation to the temperatures experienced during the longer periods lizards are not actively thermoregulating has taken place. Also, Bennett & Dawson (1976) based their analysis on measurements derived from many independent studies. Differences in experimental procedures and techniques (see Chapter 2.1) between these separate studies may have introduced an unpredictable level of variation into the data which may have been sufficient to obscure any trends due to metabolic adaptation.

During the course of the present study the SMLs of a large number of species from different thermal environments were collected. These data clearly demonstrate that there are distinct metabolic levels among the lizards which cannot just be explained in terms of anatomical differences between genera. It was therefore decided to re-examine the relationships between SML, PBT and thermal environment using data obtained from consistently applied procedures and techniques.

6.2 MATERIALS AND METHODS

6.2.1 Animals

The lizards used, and their maintenance and feeding, are as previously described (Chapter 2.2.1). All animals were acclimated to an environmental temperature of 30°C before determinations of either oxygen consumption or PBT were made.

6.2.2 Determinations of standard metabolic level (SML)

The collection of data and calculation of SMLs at 30 and 37°C are described in Chapter 2. SMLs were not measured directly at the lizards' PBT but were calculated from the 30 and 37°C SMLs of each species, using the Q_{10} relationship. Considerable confidence can be attached to these estimates since the PBT of most species examined actually fell between 30 and 37°C, and therefore within the temperature range across which the Q_{10} values were calculated. For species from which measurements were only made at 30°C the SML at their PBT was estimated using the mean Q_{10} value of 2.36.

6.2.3 Determinations of preferred body temperature (PBT)

The PBTs of lizards were determined in a thermal gradient using the same equipment and procedures described in Chapter 5.2.2. The only difference was that specimens of the larger and more aggressive species, such as *Varanus griseus* and *Agama stellio*, were placed individually into the gradient.

6.2.4 Thermal environment

A strictly quantitative examination of the relationship between SML or PBT and climate is not possible, since a single value adequately describing the environmental temperatures experienced by the reptile

cannot be produced. This is because the temperature encountered by different individuals will vary both temporally and spatially across the geographical range of the species. Also, the quantitative use of climatic data is inappropriate since it does not necessarily describe the microclimates occupied by the lizards. However, it is possible to compare, in general terms, the SMLs and PBTs of species from different geographical and climatic regions.

Lizards were placed into one of two broad geographical categories, each of which was further sub-divided into two groups:

I. Europe

This region encompasses a wide range of cold and warm temperate climates, between 35 and 70°N latitude. Mean annual temperatures range from approximately 0 to 20°C, and all regions are seasonal to varying degrees.

a) Northern Europe

Although they overlap with some of the other species in central Europe, the distribution of these lizards extends much further north into Britain and Scandinavia. At the northern limits of their ranges they experience a subarctic climate, with mean January and July temperatures below -10 and 10°C, respectively. These species are only active during the summer months.

b) Central and Southern Europe

These species are confined to warmer area of Europe, south of about 50°N latitude, where mean January temperatures are above 0°C, and July 20°C. Most areas show wide seasonal variations in temperature. In cooler regions lizards may be dormant for part of the year.

Table 6.1 Allocation of the lizard species used in the present study to geographical and climatic regions (for details see text 6.4.2)

Geographical region	Species	Microclimate
I EUROPE		
(a) North	Lacerta vivipara	T
	Anguis fragilis	F
(b) Central & South	Lacerta sicula	T
	Lacerta muralis	T
	Lacerta lilfordi	T
	Lacerta viridis	T
	Lacerta lepida	T
	Chalcides chalcides	F
II AFRICA		
(a) North	Scincus scincus	T
	Chalcides ocellatus	T
	Tarentola mauritanica	N
	Agama stellio	T
	Chamaeleo chamaeleon	A
	Varanus griseus	T

T: Diurnal, predominantly terrestrial

A: Diurnal, arboreal

F: Fossorial

N: Nocturnal

Table 6.1 (continued)

Geographical region	Species	Microclimate
II AFRICA (continued)		
(b) East & South	Cordylus jonesi	T
	Cordylus vittifer	T
	Cordylus warreni	T
	Cordylus giganteus	T
	Varanus exanthmaticus	T

T: Diurnal, predominantly terrestrial

A: Diurnal, arboreal

F: Fossorial

N: Nocturnal

II. Africa

Lizards from this tropical region, lying within 35° north and south of the Equator, experience warmer and less seasonal climates than European species, with mean annual temperatures varying from 20 to 25°C.

a) Northern Africa and the Middle East

These low latitude desert lizards are exposed to the highest mean summer temperatures, reaching in excess of 30°C, of all the species examined in the present study. However, mean January temperatures may fall below 15°C, and there are often considerable 24-hour variations in temperature exceeding 20°C. The distribution of some of these species also extends into Asia Minor.

b) Eastern and Southern Africa

These southern hemisphere species are from relatively arid savannah and semi-desert environments. Although throughout much of this region summer temperatures are slightly below those experienced by category IIa, there is less seasonal variation with July (winter) temperatures averaging over about 20°C.

Species were allocated to the category which encompassed the majority of their range (Table 6.1), although there was some overlap even between these broad groups. For example, some of the North African species also have more restricted distributions on the coastal regions of Mediterranean Europe and in the Iberian Peninsula.

Further problems are encountered in categorising the microclimate of individual species within each environment. Although *Chamaeleo chamaeleon* and *Tarentola mauritanica* are the only arboreal and nocturnal species, respectively, examined in the present study, it is more

difficult to classify burrowing or fossorial forms. Many lizards, particularly scincids, spend varying amounts of time below the surface, however, the only specialised snake-like burrowing forms examined were *Anguis fragilis* and *Chalcides chalcides*.

6.3 RESULTS

All 12 species examined behaviourally thermoregulated when placed in a temperature gradient. The PBTs of these species, together with those of *Lacerta vivipara* (Avery, 1971) and *Anguis fragilis* (Spellerberg, 1976) which were not measured in this study, are shown in Table 6.2. The SMLs of these, and an additional 5 species of which the PBTs were not determined, at 30°C and, where appropriate, their respective PBTs are also presented. The PBTs obtained from these lizards show good agreement with those of related species in the existing literature. *Lacerta viridis* was found to have a PBT of 32.6°C, a value similar to that of 32.0°C produced by Saint-Girons & Saint-Girons (1956) for this species. The PBTs of *Scincus scincus* and *Chalcides ocellatus* both lie within the range of 32 to 35°C previously reported for several other genera of tetrapodous scincids (Dawson, 1960; Licht *et al*, 1966; Wilson, 1971; Withers, 1981). The 37.3°C PBT of *Agama stellio* is similar to those of members of the Australian agamid genus *Amphibolurus* (Bradshaw & Main, 1968; Wilson, 1971). Earlier studies of varanids have also reported high PBTs, like that obtained here from *Varanus griseus*, in the range 35 to 38°C (Bartholomew & Tucker, 1964; Bennett, 1972a; McNab & Auffenberg, 1976; Gleeson, 1981). It has previously been recognised that many nocturnal gekkonids regulate at relatively low body temperatures (Brattstrom, 1965; Licht *et al*, 1966; Pianka & Pianka 1976) and the measured PBT of *Tarentola mauritanica* was only 28.7°C. There are no known published data with which the PBTs of *Chamaeleo chamaeleon* and the two species of *Cordylus* can be compared. Of these the PBTs of the cordylids, 33.9 and 34.2°C, were lower than was anticipated for these tropical African lizards. As already described in Chapter 2.3.1, body temperatures as

Table 6.2 Preferred body temperatures (PBTs) of lizards and their standard metabolic levels (SMLs) calculated at 30°C and their respective PBTs.

Geographical region	Species	PBT, °C (mean (± SE, n)	SML	
			30°C	PBT
Ia	Lacerta vivipara	30.2*	0.174	0.177
	Anguis fragilis	23.0**	0.125	0.117
Ib	Lacerta sicula	32.2 (± 0.3, 47)	0.176	0.213
	Lacerta muralis		0.168	
	Lacerta lilfordi	33.7 (± 0.2,116)	0.166	0.228
	Lacerta viridis	32.6 (± 0.2, 72)	0.174	0.212
	Lacerta lepida	34.2 (± 0.3, 26)	0.192	0.260
	Chalcides chalcides		0.214	
IIa	Scincus scincus	34.3 (± 0.3, 33)	0.147	0.216
	Chalcides ocellatus	33.5 (± 0.4, 47)	0.126	0.169
	Tarentola mauritanica	28.7 (± 0.6, 26)	0.097	0.087
	Agama stellio	37.3 (± 0.3, 32)	0.185	0.351
	Chamaeleo chamaeleon	32.3 (± 0.4, 24)	0.230	0.281
	Varanus griseus	37.4 (± 0.4, 11)	0.150	0.299
IIb	Cordylus jonesi	33.9 (± 0.1, 189)	0.096	0.132
	Cordylus vittifer	34.2 (± 0.3, 47)	0.099	0.149
	Cordylus warreni		0.108	
	Cordylus giganteus		0.110	
	Varanus exanthmaticus		0.157	

*Avery (1971)

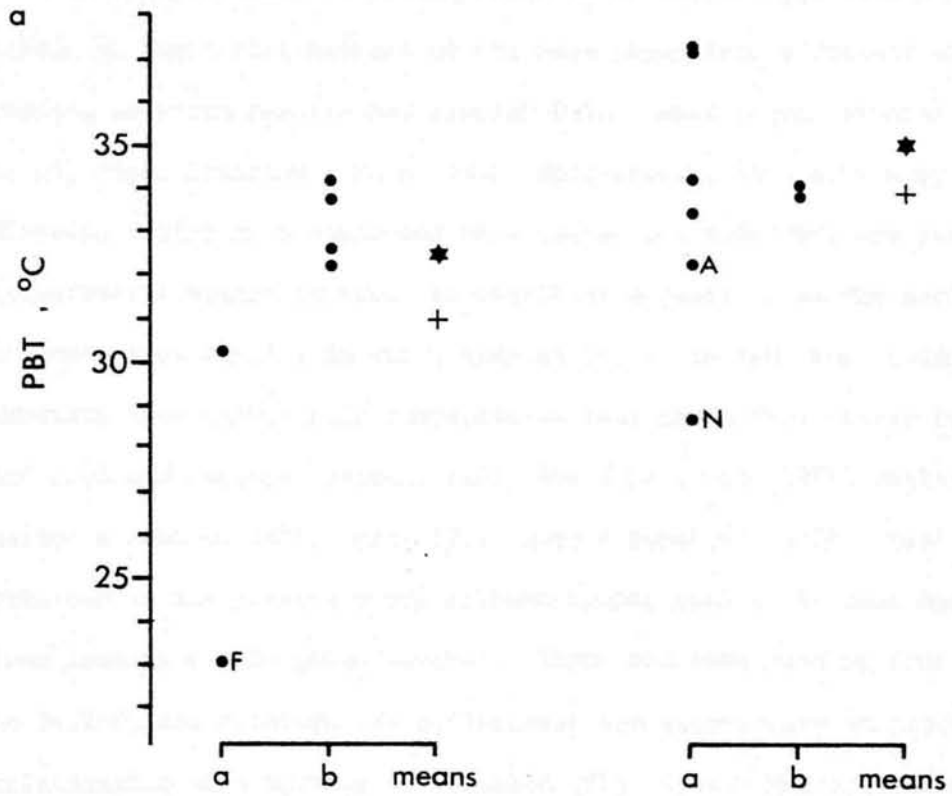
**Spellerberg (1976)

low as 37°C were fatal to another species, *Cordylus warreni*, on two occasions.

The overall mean PBT of the 8 African lizards was 34.0°C, a value not significantly ($p > 0.05$) higher than the 31.0°C mean of the 6 European species (Fig. 6.1a). When lizards occupying specialised thermal microclimates are excluded from the analysis, and comparisons are confined to the 6 African and 4 European diurnal terrestrial species, the mean PBTs of 35.1 and 32.6°C, respectively, are significantly different ($p < 0.05$).

The 11 African and 8 European lizards have overall mean SMLs at 30°C of 0.137 and 0.185, respectively (Fig. 6.1b). These values are 0.131 and 0.175 for the 9 African and 6 European diurnal terrestrial species alone. In both cases the differences are significant ($p < 0.01$), with the SMLs of African lizards only approximately 74% of those from Europe.

Fig. 6.1


a
PBT , °C
35
30
25
F
A
N
a
b
means
I EUROPE
II AFRICA

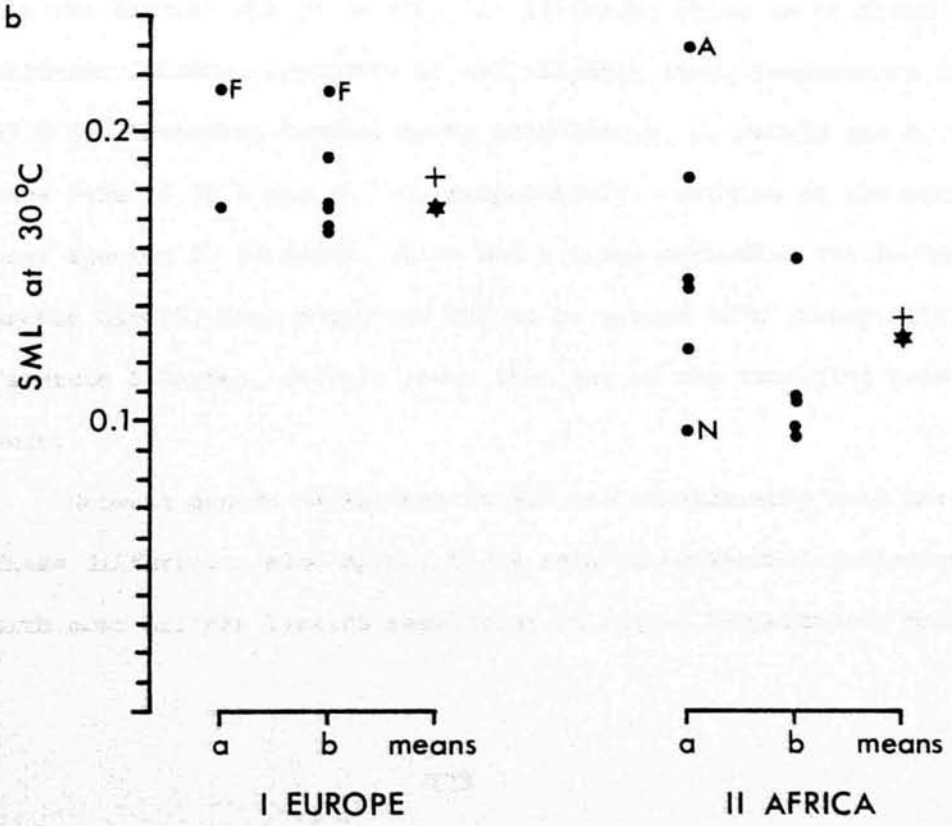

b
SML at 30 °C
0.2
0.1
F
F
A
N
a
b
means
I EUROPE
II AFRICA

Figure 6.1 (a) Preferred body temperatures (PBTs), and (b) standard metabolic levels (SMLs), in relation to geographical distribution in European and African lizards. Means quoted were calculated from the data relating to (+) all, and (*) diurnal terrestrial species only, for each of the two major geographical regions.

6.4 DISCUSSION

6.4.1 The relationships between PBT and thermal environment

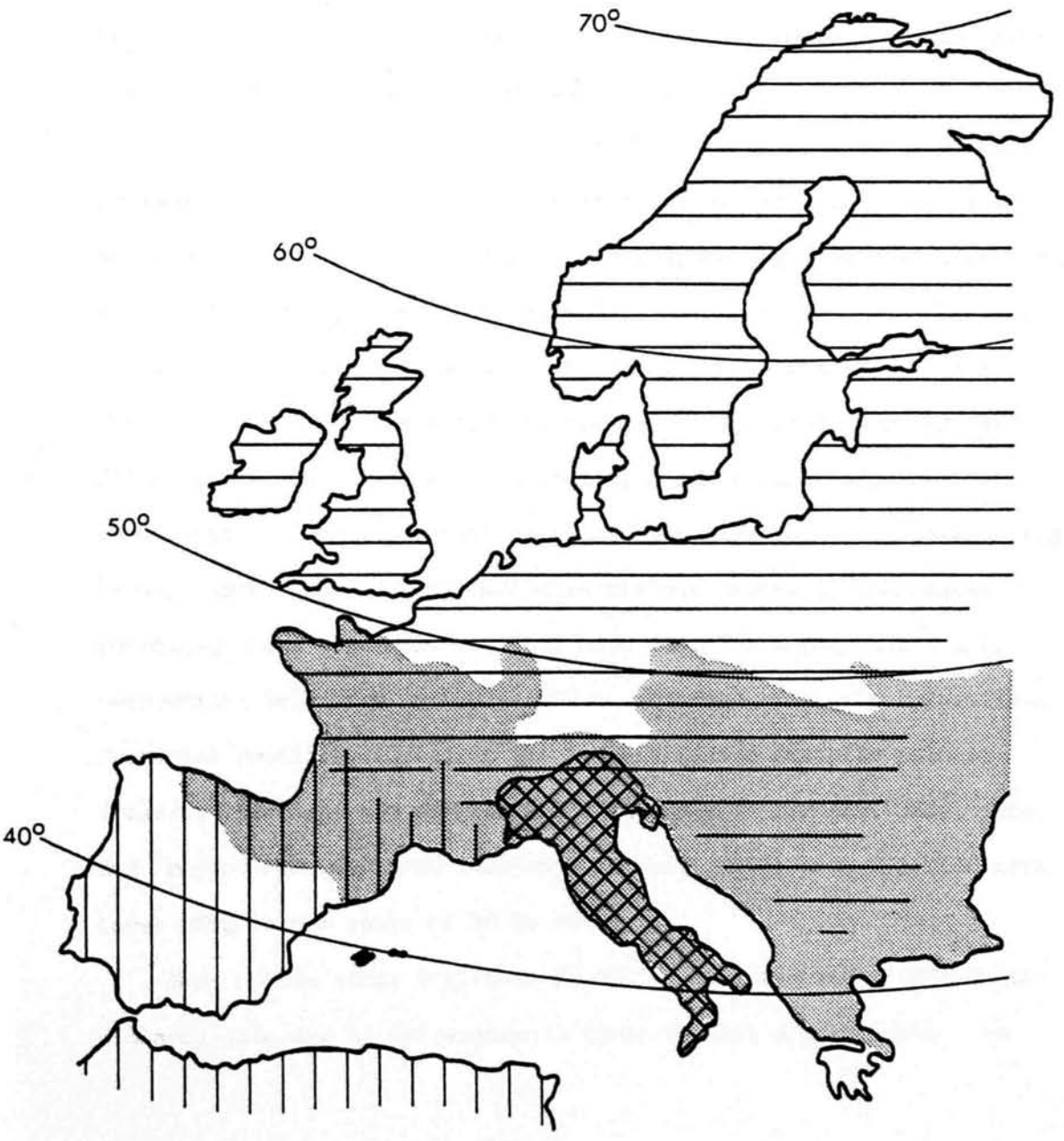
In early studies of lizard behavioural thermoregulation Bogert (1949a,b) found that members of the same genus from different climatic regions of North America had similar PBTs. More recent studies (Licht *et al*, 1966; Bradshaw & Main, 1968; Spellerberg, 1972 a,b; Huey & Slatkin, 1976b) have supported this contention that PBTs are generally conservative within genera. An exception appears to be the ecologically diverse genus *Anolis*, in which species living in open and lowland habitats have higher body temperatures than those from cooler forested and highland regions (Ruibal, 1961; Heatwole *et al*, 1969; Ballinger, Marton & Sexton, 1970; Corn, 1971; Huey & Webster, 1976). Data obtained in the present study allowed comparisons to be made between four species of the genus *Lacerta*. These had PBTs ranging from 32.2 to 34.2°C, and although the differences are slight they do suggest a relationship with thermal environment (Fig. 6.2). The species with the southernmost distribution, *L. lepida* from Iberia and north-west Africa, has the highest PBT of 34.2°C. *L. lilfordi*, which is confined to the Balearic Islands, regulates at the slightly lower temperature of 33.7°C. Extending further north into Europe, *L. sicula* and *L. viridis* have PBTs of 32.2 and 32.6°C, respectively. Studies on the northern-most species *L. vivipara*, which has a range extending inside the Arctic Circle, have found its PBT to be around 30°C (Avery, 1971; Paterson & Davies, 1978a), lower than any of the lacertids measured here.

Between genera variations in PBT are considerably more marked. These differences also appear to be related to thermal environment, with most African lizards regulating at higher temperatures than those

Figure 6.2 Geographical distribution, preferred body temperatures (PBTs) and standard metabolic levels (SMLs) of six European lizards of the genus *Lacerta* (see Table 6.2).

Fig. 6.2

	PBT	SML at 30°C
Lacerta vivipara	30.2 °C	0.174
L. sicula	32.2 °C	0.176
L. viridis	32.6 °C	0.174
L. lilfordi	33.7 °C	0.166
L. lepida	34.2 °C	0.194



from Europe (Fig. 6.1a). The temperate lacertids already discussed possessed the lowest PBTs of diurnal terrestrial species, although the mean of the South African cordylids was only slightly greater. The highest PBTs measured were those of *Agamo stellio* and *Varanus griseus*, at 37.3 and 37.4°C respectively, two large desert species which experience the warmest diurnal summer temperatures. A study of the lizard faunas of Western Australia also showed that genera inhabiting hotter environments generally have higher PBTs (Licht *et al*, 1966). A similar trend exists in the south-western U.S.A., where the average PBT of lizard species at a given locality was found to correlate with long-term mean July temperature (Huey & Slatkin, 1976).

Species which spend less time on the surface display lower PBTs, presumably as a direct consequence of their reduced access to direct solar radiation. Although higher than temperate European species, the PBTs of the two North African scincids, *Scincus scincus* and *Chalcides ocellatus*, were lower than those of the sympatric agamid and varanid. The PBTs of the two snake-like burrowing forms, *Anguis fragilis* and *Chalcides chalcides*, were not measured, however other studies have shown that *A. fragilis* possesses a low PBT of around 23°C (Spellerberg, 1976). Among South African scincids the monodactylous and legless burrowing forms were also found to have lower PBTs than their more terrestrial relatives (Withers, 1981). Studies of highly specialised fossorial reptiles, including the legless lizard *Anniella pulchra* (Fusari, 1984) and the amphisbaenids *Amphisbaena mertensi* (Abe, 1984) and *Trogonophis wiegmanni* (Gatten & McClung, 1981) have reported even lower PBTs in the range of 20 to 24°C.

Some of the other variation in PBT between sympatric lizards is probably also due to differences in their thermal microclimate. For

example, *Chamaeleo chamaeleon* possessed the lowest PBT of the diurnal north African species examined in this study. This could be related to their predominantly arboreal mode of life, since living in vegetation they experience lower temperatures than on the ground surface. Nocturnal lizards, like fossorial species, do not have access to any significant direct radiant heat, and are generally active when ambient temperatures are low. This and other studies have found that many gekkonids regulate in the range 20-30°C, body temperatures considerably lower than those of most diurnal forms. (Brattstrom, 1965; Licht *et al*, 1966; Bustard, 1967; Pianka & Pianka, 1976).

Therefore, it appears that the PBT of a species is related to the environmental temperatures it experiences during activity. However, it should be noted that the variations in PBTs of species examined in the present study are considerably less both within and between genera, than the differences in temperature of their respective natural environments.

6.4.2 The relationships between SML and body temperatures

Metabolic adaptation could be a response to the temperatures experienced during either the active or inactive phase of the animals. If adaptation compensates for differences in the body temperature of lizards while they are actively thermoregulating then SMLs, determined at the same temperature, should be inversely related to PBT. Complete compensation would result in all species possessing similar SMLs when measured at their respective PBTs. Bennett & Dawson (1976) calculated the metabolic levels of 19 species of lizards at their appropriate PBTs and found that, rather than being approximately the same, these estimates were still related to body temperature by a Q_{10} of 2.4. Since this value is no different from those reported within species they

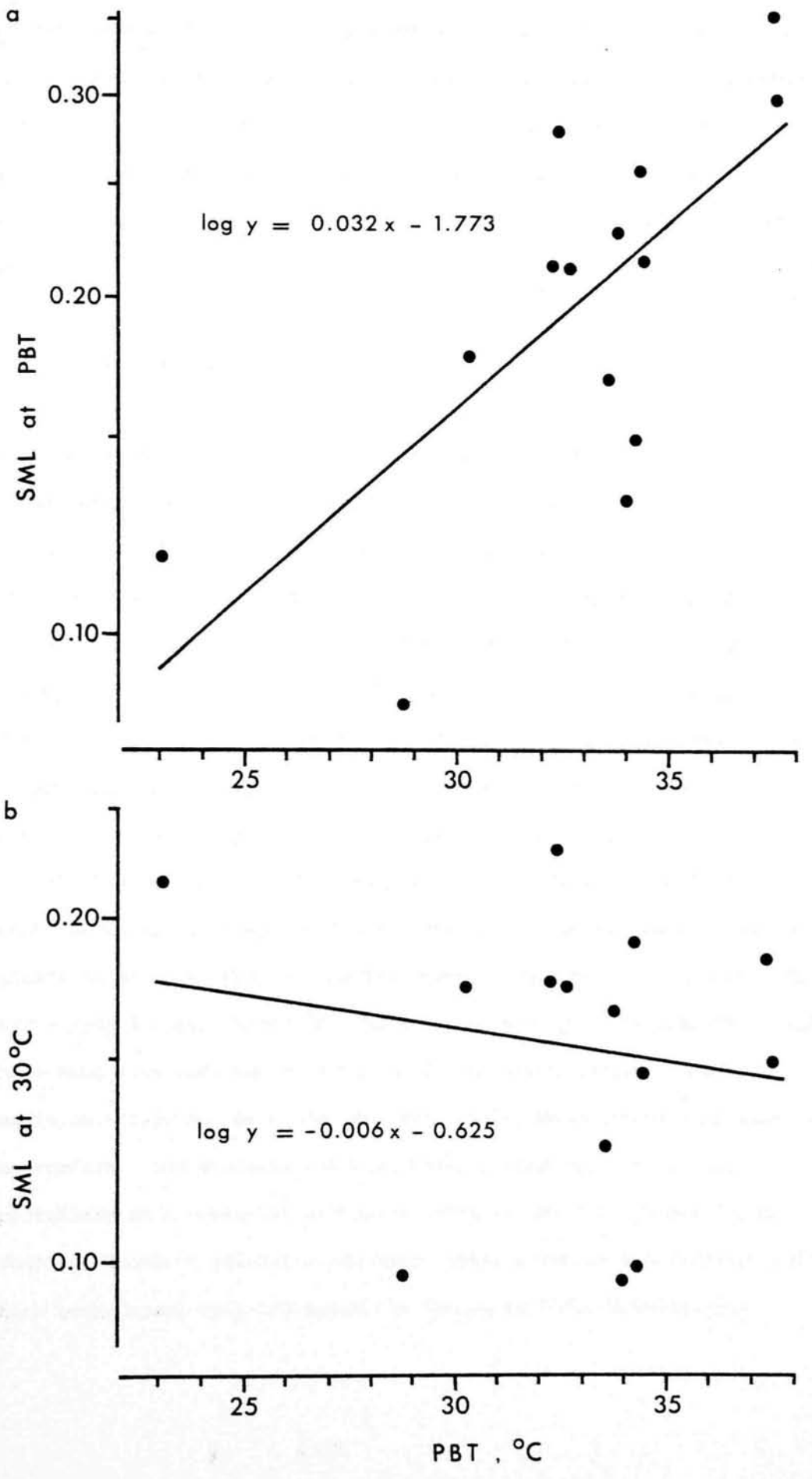
therefore concluded that there was no evidence of any adjustment of metabolic level to PBT. A similar regression analysis (Fig. 6.3) of the metabolic data obtained under standard conditions in the present study produced a slope of 0.0324 (n = 14; r = 0170; 95% c.l. of slope = ± 0.0211), which corresponds to a Q_{10} of 2.11 (Fig. 6.3a). This is not significantly different ($p > 0.05$) from the mean value for individual species of 2.36 (Chapter 2.3.3), which also indicates that little, if any, compensation has occurred. When the SMLs of these species at a constant body temperarure of 30°C are regressed against PBT (Fig. 6.3b) there is a slight inverse relationship (slope = -0.0058; n = 14; r = -0.17; 95% c.l. of slope = ± 0.0215), although this is not significant ($p > 0.05$).

Of the species occupying more specialised thermal microclimates, the burrowing *Anguis fragilis* and arboreal *Chamaeleo chamaeleon* conform to the expected pattern by possessing both a relatively low PBT and high SML. However, the nocturnal gekkonids and xantusids (Bennett & Dawson, 1976) which also have low PBTs, do not have correspondingly high metabolic levels. Conversely, *Tarentola mauritanica* displayed one of the lowest SMLs of all the species examined in the present study.

It therefore appears that there is no overall relationship between SML and PBT among lizards. However, the observed metabolic differences could be adaptations to the wider range of temperatures experienced during the period they are not thermoregulating. As discussed in Chapter 2.3.3 SMLs appear to be conservative within the genera *Lacerta* and *Cordylus*, and consequently little evidence would be expected of compensation among members of either genus. There is no consistent geographical trend to the slight variations of lacertids (Fig. 6.2),

Figure 6.3 Relationships between standard metabolic levels (a) calculated at the appropriate preferred body temperature (PBT), and (b) measured at 30°C, and the PBT of the lizard. Lines were fitted by linear regression analysis.

Fig. 6.3


a
0.30
0.20
0.10
SML at PBT
log y = 0.032 x - 1.773
25
30
35
b
0.20
0.10
SML at 30°C
log y = -0.006 x - 0.625
25
30
35
PBT , °C

and sufficiently detailed information on the distribution of the four *Cordylus* species is not available to explore any possible relationships in this genus. The two members of the genus *Chalcides* examined possessed significantly different SMLs. As would be predicted, the more temperate and fossorial species, *Chalcides chalcides*, has the higher SML. However, it should be noted that, unlike the lacertids and cordylids, there are also marked anatomical differences between these two species of sincids (Chapter 2.3.3).

Inter-generic differences in SML are considerably greater than those found within genera, and there is evidence of adaptation to thermal environment at this taxonomic level. Dawson and co-workers (Dawson, 1960; Dawson & Bartholomew, 1958; Dawson & Templeton, 1963, 1966) found that at high temperatures the two thermophilic desert genera *Crotaphytus* and *Dipsosaurus* displayed weight specific oxygen consumption rates below those of *Eumeces* and *Gerrhonotus*, two lizards of comparable body mass from cooler environments. In the present study the African lizards examined possessed a mean SML significantly lower than that of the temperate European species (Fig. 6.1b).

Although burrowing forms would be expected to have relatively high metabolic levels to compensate for their cooler microclimate, there appears to be no simple relationship between this mode of life and SML. *Anguis fragilis* and *Chalicides chalcides* do both possess high SMLs, and these have also been reported for other burrowing anguids (Dawson & Templeton, 1966) and scincids (Withers, 1981), which spend some time on the surface. The opposite has been found in species more highly specialised to a fossorial existence, such as *Anniella pulchra* (Fusari, 1984) and *Acontias meleagris* (Withers, 1981; Brownlie & Loveridge, 1983), which both posses very low metabolic levels at 30°C. However, the

metabolism of these species will not be as low, with respect to other lizards, at the cooler temperatures they experience under natural conditions as they are at 30°C since they also possess low Q_{10} values. The high SML of *Chamaeleo chamaeleon* is consistent with the lower temperature of its arboreal microclimate.

Nocturnal lizards which experience relatively cool environmental temperatures might also be expected to possess high SMLs. As already discussed, the metabolic levels of many nocturnal gekkonids, including *Tarentola mauritanica*, and xantusids (Vance, 1959; Snyder, 1971) are very low. The sole surviving rhynchocephalian, the tuatara *Sphenodon punctatus*, also exhibits low resting oxygen consumption rates (Wilson & Lee, 1970) which suggests that a reduced metabolic level may be a general characteristic of nocturnal reptiles. The answer to this apparant anomaly could be that because these species are active at night they consequently experience higher body temperatures while inactive during the day than do diurnal species, which rest at night. This indicates that lizards might adapt to compensate for differences in the environmental temperatures they experience during their inactive phase, regardless of when in each 24-hour cycle this occurs.

It is not possible to separate completely the extent to which any metabolic compensation is a response to differences in PBT or the temperature of the environment since, as already discussed, both factors are themselves related. However, the relationship between SML and the environmental temperatures encountered by inactive reptiles appears most consistent. This suggests that the role of this adaptation in lizards is probably to reduce the metabolism of resting animals, rather than to compensate for differences in their PBT during the period they are behaviourally thermoregulating.

Although the differences in metabolic level appear to be adaptative, it is possible that they also reflect physiological and anatomical factors. For example, the high oxygen consumption of *Chamaeleo chamaeleon* could be to compensate for its cooler arboreal microclimate or, as discussed in Chapter 2.3.3, a consequence of the muscle tonus required to maintain its upright posture. Also, the well developed, and relatively metabolically inert, dermal armour of cordylids could contribute to their low SMLs. However, this cannot be the only reason for the low metabolic levels of these lizards, since the oxygen consumption rates of isolated liver tissue were less than those of temperate lacertids (see Chapter 4.3.3). Therefore the variations in SML between lizard genera are probably the consequence of a combination of ecological, physiological and anatomical differences.

6.4.3 Summary

In lizards it appears that evolutionary adaptation is the major means of achieving compensation of both SML and PBT to thermal environment. As discussed in Chapter 5, acclimatory responses by an individual to seasonal changes in temperature are more limited; PBT appears to be fixed and the extent to which shifts in metabolic level can be induced is fairly limited. Interpreting the significance of these responses is less straightforward than for the more extensively studied aquatic bradymetabolic organisms, which remain isothermal with their surroundings. However, if their thermal requirements during the active and inactive phases are considered separately it is possible to produce a tentative explanation of adaptative and acclimatory strategies in lizards (Fig. 6.4).

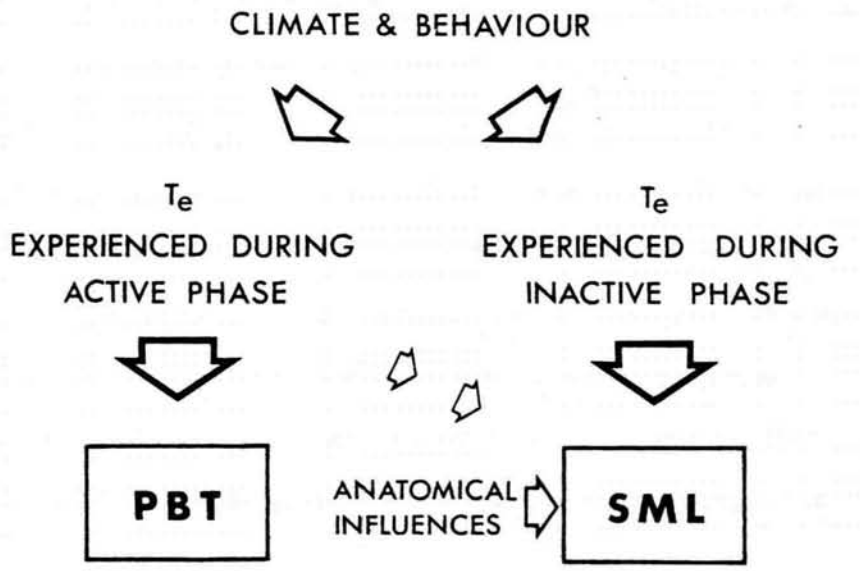
(a) Active phase

Although lizards inhabiting relatively thermally homogeneous environments, such as tropical rain forests, are unable to exert any significant control over their body temperature (Hertz, 1974; Huey, 1974; Huey & Webster, 1975), species in more heterogeneous habitats usually behaviourally thermoregulate, often with considerable precision. Species experiencing warmer microclimates while active generally maintain higher PBTs. Although adaptative differences in PBT do exist between the members of some genera there is greater inter-generic variation. There appear to be particular advantages associated with higher PBTs, since many cool temperate species expend considerable effort in regulating well above ambient temperature (Pearson, 1954; Avery, 1971; Spellerberg, 1976). This results in the range of PBTs exhibited by lizard species being less than that of the temperatures of their respective environments.

The advantages to a lizard of maintaining such a high relatively constant body temperature are not immediately evident. It obviously cannot be to conserve energy, since this would favour the selection of lower temperatures. Neither can the only benefit be general metabolic homeostasis, since this could be achieved at lower, more easily maintained, PBTs. Also, the fluctuations in SML induced in many species by acclimation to seasonal changes in temperature (Chapter 5.4.2) suggest that the maintenance of precise metabolic homeogeneity during their active phase is not critical to lizards.

However, the physiological processes associated with locomotion and behaviour will be of crucial importance to the active animal. Therefore, the influence of temperature on the functioning of the neuromuscular and central nervous systems may have particular relevance. Unlike the

Fig. 6.4



ACCLIMATORY RESPONSES (SEASONAL)	Fixed	a) Relatively small compensatory (Type 3) shifts in continually active species. b) Inverse (type 5) compensation in hibernating species. (Probably induced by combined influences of temperature and photoperiod change.)
ADAPTATIVE RESPONSES (EVOLUTIONARY)	Higher in species experiencing warmer microclimates during activity.	Lower in species experiencing warmer microclimates while at rest.
POSSIBLE STRATEGIES	Increase in speed of CNS functioning and capacity of locomotor system, enabling more complex sustainable behaviours	Energy conservation (Water conservation?)

Figure 6.4 Summary diagram of the proposed influences of environmental temperature on the preferred body temperature (PBT) and standard metabolic level (SML) of lizards.

earlier findings of Licht (1964a) and Licht, Dawson & Shoemaker (1969), the more recent study of Putnam & Bennett (1982) reported the isometric twitch and tetanic tensions of reptilian muscle are broadly temperature independent. However, they did show that the speed of twitch and maximal rate of tension development both increased with temperature. In three of the four species examined the rate of maximal tension development, which is an indicator of the optimisation of both contractile speed and tension, was greatest at temperatures close to their PBTs. Licht (1946b) reported that the temperatures at which skeletal muscle ATPase activities are maximal are also adapted to PBT. Since it is therefore possible for some species to achieve optimal muscle performance at their lower body temperatures it suggests that there must be additional advantages afforded to those which regulate at higher PBTs.

Some energetic aspects of reptilian locomotion are also temperature dependent. Although anaerobic capacity is not strongly influenced by temperature (Bennett & Licht, 1972), within species aerobic scope increases with body temperature (Bennett, 1982, 1983). In most species there is a metabolic plateau or decline in oxygen consumption at temperatures above PBT (Dawson, 1975; Bennett & Dawson, 1975), although in varanid lizards maximal aerobic capacity continues to increase above this temperature (Bartholomew & Tucker, 1964; Bennett, 1972a). This greater metabolic capacity allows lizards to maintain faster maximum walking speeds at higher temperatures (Moberly, 1968; John-Alder & Bennett, 1981). Although thermoregulating at a high PBT therefore increases the range of speeds and behaviours a lizard can sustain, there are associated energetic costs since SML is greater and locomotion at any speed more expensive at higher temperatures (John-Alder &

Bennett, 1981).

In comparison with locomotory physiology, far less work has been conducted on the thermal dependence of neurological function in reptiles. There are good reasons why body temperature might have a profound influence on the functioning of the central nervous system (CNS), since both the speed of action potential propagation and synaptic transmission are temperature dependent. Consequently, at higher temperatures the CNS of an animal will be able to process information faster, or alternatively undertake more sophisticated processing in the same amount of time. Therefore, a species which thermoregulates at a high PBT should be able to interact more rapidly and in more complex ways with its environment, which will be extremely advantageous to its feeding, predator avoidance and social behaviours. This is consistent with the observation (Avery, 1976) that complex social behaviours are most highly developed in lizards from warmer climates. However, there are limits to the extent to which CNS performance can be increased by raising body temperature because nervous tissue is particularly susceptible to damage by hyperthermia. Consequently reptiles have evolved physiological mechanisms which enable them to reduce fluctuations in brain temperature below those experienced by the rest of the body (Heath, 1964, 1966; De Witt, 1967; Webb, Johnson & Firth, 1972; Johnson, 1972). Therefore, CNS functioning is an important aspect of the lizards' biology for which the maintenance of both a high and accurately regulated PBT during activity will be extremely important.

(b) Inactive phase

The observed differences in SML between species indicate that adaptative compensation to the environmental temperatures experienced during the lizards' inactive phase has taken place. That SML is more strongly influenced by the animal's resting body temperatures than its PBT is consistent with the finding (Chapter 5.4.2) that these are also the temperatures to which they acclimate. The idea that it is advantageous for resting lizards to minimise their metabolism is strongly supported by the observation in the present study (Chapter 5.2.2) and by Regal (1967), that when individuals are not actively thermoregulating they always move to the cooler regions of a thermal gradient. During these periods of inactivity any reduction of CNS and neuromuscular performance resulting from the lower body temperature will be of limited importance to the animal.

There are at least two reasons why a reduced metabolic rate could be of benefit to a resting lizard, neither of which are mutually exclusive. One explanation is that it is simply a strategy for conserving energy. A second possibility is that the reduced rate of gaseous exchange required by a lower SML helps to restrict respiratory water loss (Snyder, 1971). This may be particularly important because many lizards, including the majority of the warm temperate and tropical species examined in the present study, inhabit relatively dry environments. A similar trend has been found among small rodents, most arid-adapted species of which posses reduced BMLs (Hart, 1971; Bradley, Miller & Yousef, 1974; Borut & Shkolnik, 1974; McNab, 1979).

The relationships between PBT, SML and thermal environment in lizards are obviously complex and it would be misleading to try and over-simplify the strategies involved. However, it is tempting to

speculate that they behaviourally thermoregulate at high relatively constant body temperatures during activity to optimise the performance of their CNS and increase the capacity of the locomotory system, despite the energetic costs involved. During the majority of each 24-hour cycle the lizard is inactive the emphasis appears to be on reducing metabolic rate to conserve energy, and possibly also water.

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APPENDIX 1

GLOSSARY OF TERMS AND ABBREVIATIONS RELATING TO THERMAL PHYSIOLOGY

Much of the terminology relating to thermal physiology is confused by ambiguity in definition and plurality of usage. This has arisen largely because when much of it was introduced all of the complexities associated with the establishment of body temperature, as well as the diversity of patterns displayed throughout the animal kingdom, were not fully appreciated. Despite the introduction of papers defining thermal terminology and semantics it is apparent that there is still no universal agreement of their application in practice. The most comprehensive glossary of terms for use in thermal physiology was produced by Bligh & Johnson (1973). However, many of the terms, as defined by this paper, are strongly orientated towards application in mammalian studies, and have limited relevance to lower vertebrates and invertebrates. For example, the terms homeothermy and endothermy are both used solely to describe the pattern of temperature regulation found in the tachymetabolic birds and mammals, which fails to appreciate the degree of thermoregulatory sophistication attained by many bradymetabolic forms (Chapter 1.1). Also, many of the terms relating to the metabolism of an animal, such as resting and basal metabolic rates, specify that it must be in a state of thermoneutrality, a concept which has no relevance to bradymetabolic organisms. Therefore, although the terminology as used in this thesis, and listed below, largely follows that of Bligh & Johnson (1973), the definitions of some of the terms have been widened to increase their applicability to reptiles.

GENERAL TERMS

HOMEOTHERMY (HOMIOTHERMY)

The ability of an organism to maintain core temperature (T_c) within arbitrarily defined limits despite much large variations in environmental temperature (T_e). Homeothermy may be maintained continually or for limited periods only. The use of this term implies nothing about the means by which T_c is regulated, or the phylogenetic status of the animal involved. (Autonym: POIKILOTHERMY).

ENDOTHERMY

The ability of an organism to produce and retain sufficient metabolic heat to raise T_c significantly above that of its surroundings (T_e). Endothermy may be maintained continually or for limited periods only, such as during activity. The use of this term implies nothing about the physiological mechanisms by which the differential between T_c and T_e is established, or the phylogenetic status of the animal involved. (Autonym: ECTOTHERMY).

TACHYMETABOLISM

The pattern of thermal physiology in which an animal possesses a relatively high BML and is able to response to a fall in T_e with an increase in regulatory heat production (RHP) to maintain homeothermy. Most tachymetabolic species are continually both homeothermic and endotermic. The only extant forms with this physiology are the birds and mammals. (Autonym: BRADYMETABOLISM).

BRADYMETABOLISM

The pattern of thermal physiology in which an animal possesses a relatively low SML when measured at a body temperature of 37°C. In bradymetabolic animals a fall in T_e simply results in a reduction of SMR. Although usually poikilothermic and ectothermic, many bradymetabolic forms are able to attain varying degrees of homeothermy and endothermy. All living lower vertebrates and invertebrates are bradymetabolic. (Autonym: TACHYMETABOLISM).

ACCLIMATION

A phenotypic change occurring within the life time of an individual which reduces the strain caused by experimentally induced changes in particular climatic factors.

ACCLIMATISATION

A phenotypic change occurring within the life time of an individual which reduces the strain cuased by changes in the natural environment.

ADAPTATION

A genetically fixed attribute of a species which reduces the strain resulting from a stressful component of the natural environment.

TEMPERATURES

AMBIENT TEMPERATURE (T_a)

The mean temperature of a fluid environment surrounding a body, as measured outside the thermal and hydrodynamic boundary layers that overlay the body.

ENVIRONMENTAL TEMPERATURE (T_e)

The temperature at which an inanimate body, of the same shape and size as an organism, will come to equilibrium with its surroundings when placed at the same point in space. Therefore, unlike T_a, this measure of temperature includes radiative and convective influences on the animal.

CORE TEMPERATURE (T_c)

The mean temperature of the tissues at a depth below that which is affected directly by a change in the temperature gradient through the peripheral tissues. T_c cannot be measured accurately and is generally represented by a specified body temperature. In this study rectal and cloacal temperatures are taken as representing T_c.

PREFERRED BODY TEMPERATURE (PBT)

The mean T_c of behaviourally thermoregulating bradymetabolic animals in an artificial temperature gradient.

MEAN BODY TEMPERATURE (MBT)

The mean T_c actually attained by behaviourally thermoregulating brady-metabolic animals under natural conditions.

THERMONEUTRAL ZONE (TNZ)

The range of environmental temperatures across which a tachymetabolic organism is able to regulate T_c solely by modulating its thermal conductance. Within the TNZ the standard metabolic rate (SMR) of the animal is at a constant minimum level, termed basal metabolic rate (BMR)

LOWER CRITICAL TEMPERATURE (T_{lc})

The environmental temperature defining the lower limit of the TNZ of a tachymetabolic animal. Below the T_{lc} the animal must generate regulatory heat production (RHP) in addition to its BMR to maintain homeothermy.

UPPER CRITICAL TEMPERATURE (T_{uc})

The environmental temperature defining the upper limit of the TNZ of a tachymetabolic animal. Above this temperature SMR rises as a consequence of an increase in T_c.

METABOLIC RATES

The Système Internationale (S.I.) unit of metabolic rate is the the Watt (W). However, in practice metabolism is usually measured by indirect calorimetry and, rather than convert to energy utilisation with an assumed conversion factor, values are often presented, as here, as rates of oxygen consumption. Where comparisons are made from other studies quoted in Kcal a conversion factor of 208.33 ml O_2/Kcal has been used.

STANDARD METABOLIC RATE (SMR)

The metabolic rate of a resting, post-absorptive animal in a darkened chamber during its photophase at a specified environmental temperature. Unless otherwise stated, reptiles were acclimated to an environmental temperature of 30°C before SMR was determined. For tachymetabolic animals SMR is the total of BMR and RHP (Units: ml O_2/h, ml O_2/g.h).

BASAL METABOLIC RATE (BMR)

The metabolic rate of a resting, post-absorptive tachymetabolic animal in a darkened chamber during its photophase under conditions of thermoneutrality (Units: ml O_2/h, ml O_2/g.h).

REGULATORY HEAT PRODUCTION (RHP)

The component of SMR, additional to BMR, produced by a tachymetabolic animal at environmental temperatures below those of thermoneutrality (Units: ml O_2/h, ml O_2/g.h).

STANDARD METABOLIC LEVEL (SML)

The total SMR (ml o_2/h) of an animal at a specified temperature divided by body mass raised to the power of the metabolic exponent for that species or taxonomic group (see Chapters 1.3 and 2.3.3).

BASAL METABOLIC LEVEL (BML)

The total BMR (ml O_2/h) of a tachymetabolic animal divided by body mass raised to the power of the metabolic exponent for that species or taxonomic group.(see Chapter 1.3 and 3.3.3).